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Role of Hurricane Disturbance in the Dynamics of the Southern Mixed Hardwood Forest: A Case Study in Northern Florida.

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ROLE OF HURRICANE DISTURBANCE IN THE DYNAMICS OF THE SOUTHERN MIXED HARDWOOD FOREST: A CASE STUDY IN NORTHERN FLORIDA

A Dissertation

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by
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Abstract

The objective of this dissertation was to characterize the role of hurricanes in the dynamics of old-growth Southern Mixed Hardwood Forests from the coastal plain of the northern Gulf of Mexico. First, we used data from five stands to describe the structure, composition, and disturbance regime of these forests. All five stands have *Magnolia grandiflora* and *Fagus grandifolia* among the dominant species, and have been affected by frequent but relatively mild hurricanes (4-6 per century, windspeed < 200 km/h). Second, we examined the changes in tree recruitment, growth, and mortality occurred in Woodyard Hammock, northern Florida, after this forest was affected by Hurricane Kate in 1985. The analysis was based on data from biennial censuses of a 4.5 ha plot conducted between 1978 and 1992. Hurricane Kate produced extensive canopy disruption but limited tree mortality. This disturbance prompted a phase of increased recruitment, growth, and survival of understory trees, and decreased growth and survival of overstory trees. Release of small understory individuals appeared to be critical for the persistence of three short-lived dominant species, *Pinus glabra*, *Ostrya virginiana* and *Carpinus caroliniana*. However, persistance of the longer-lived dominants *Magnolia grandiflora*, *Fagus grandifolia*, *Liquidambar styraciflua*, *Nyssa sylvatica*, and *Ilex opaca*, appeared to depend primarily on resistance to hurricane damage. Third, we used matrix population models to test specific hypotheses about mechanisms of persistence of *F. grandifolia* in Woodyard Hammock. These models showed that, both before and after Hurricane Kate, this population was close to equilibrium. This result supported the hypothesis that persistence of *F. grandifolia* has resulted from

hurricane resistance. Sensitivity analyses of the models suggested that the key for hurricane resistance has been the high survival of medium-size trees. Life-history strategies involving resistance and survival to hurricane disturbance, rather than release and rapid growth, appear to have been prevalent in these forests. However, the hurricane regime would have resulted in coexistence of species with the two types of strategy. Hurricanes would wave been frequent enough to secure the persistence of species dependent on release, and mild enough not to compromise that of species dependent on resistance.

General Introduction

The Southern Mixed Hardwood Forest is a type of mesic temperate forests that occur along the southeastern Coastal Plain of the United States (Quarterman and Keever 1962). Typically, old-growth stands of this forest type are restricted to bands along the mid-slopes of river banks or lake terraces (Marks & Harcombe 1981, Schafale & Harcombe 1983, Platt & Schwartz 1990, Ware et al 1993). These forests have a diverse overstory stratum, usually dominated by *Fagus grandifolia* and *Magnolia grandiflora*, and an also diverse understory containing small individuals of overstory species and a set of small-stature understory species (Quarterman and Keever 1962, Monk 1967, Christensen 1988, Marks and Harcombe 1975, Platt and Schwartz 1990, Vankat 1990).

Forests similar to these would have occurred along the northern Gulf of Mexico continuously since the Miocene, and served as refuge for northern temperate species during the Pleistocene glaciations (Davis 1981, Delcourt and Delcourt 1987, Webb 1990). Early studies of the Southern Mixed Hardwood Forest portrayed it as a "climax" resulting from autogenic succession following abandonment of old-fields or fire suppression in pine savannas (Gano 1917, MacGowan 1937, Kurz 1944, Braun 1950, Quarterman and Keever 1962, Monk 1965, 1967, 1868, Delcourt and Delcourt 1974,1977, Blaisdell et al. 1974, Ware et al. 1993). This concept, however, did not include a recurrent allogenic influence acting on the dynamics of these forests: the chronic hurricane disturbance (Harcombe and Marks 1978, Glitzenstein et al 1986, Platt and

Schwartz 1990, Neumann et al. 1992, Bill and Harcombe 1994, Quigley and Platt 1996).

Woodyard Hammock is a 30-ha forest tract that stretches along the northern edge of Lake Iamonia in northern Florida, waving between the lake shore and clay hills that lay to the north. As the terrain is relatively flat, the band of Southern Mixed Hardwood Forest is very broad. Part of a plantation established in the early 1800's, Woodyard Hammock has been a part of Tall Timbers Research Station since 1959 (Blaisdell et al. 1974, Hirsh 1981, Platt and Hermann 1986, Platt and Schwartz 1990). Although in the early 1900's dead trees were salvaged for firewood and some large *Pinus taeda* were cut, this forest has never been cleared in historical times. In 1978, Bill Platt, Don Hirsch, and Steve Rathbun established a 4.5-ha permanent study plot in the middle of Woodyard Hammock where human perturbation had been minimal (Hirsh 1981, Platt and Hermann 1986). On November 21, 1985, the eye of Hurricane Kate passed within 30 km of Woodyard Hammock, exposing the forest to gusts of wind up to 160 km/h for about eight hours (Clark 1986). This was not a rare event; a total of four tropical storms of comparable intensity have passed near Woodyard Hammock since 1886. The data from the plot, which has been censused biennially since it was established, provided an exceptional opportunity to examine the role of hurricane disturbance in the dynamics of the Southern Mixed Hardwood Forest.

The general objective of the research we report here was to assess to what extent the structure and composition of Southern Mixed Hardwood Forests is controlled by recurrent hurricane disturbance. Throughout our study, we assumed that hurricane disturbance has been a consistent element of the

regional environment, and that the tree species in these forests must develop strategies allowing them to persist in the long term in the presence of such disturbances. Therefore, we assumed that tree populations would either resist hurricanes or benefit from hurricane disturbance. These two alternative strategies would be associated respectively with adaptations resulting in high tree survival, and with adaptations resulting in rapid response by released understory individuals.

In the first chapter of this dissertation we elaborated an old-growth definition for the Southern Mixed Hardwood Forest of the coastal plain of the northern Gulf of Mexico. For this definition, we characterized the structure and composition of these forests, delineated their regional and local variations, and described the disturbance regime that has affected them. In the following chapters we focused on the Woodyard Hammock data. The analyses were done at the forest-stand level, and based on censuses from the period spanning seven years before and seven years after Hurricane Kate (1978 - 1992). In the second chapter, we described the changes in recruitment, growth, and mortality of the dominant tree species in Woodyard Hammock, and we examined the associations between abundance of these species and their performance in the understory and overstory strata. These analyses were used to assess the relative importance of strategies involving resistance and tree survival as opposed to strategies involving release and rapid growth for the persistence of the dominant tree species. In the third chapter, we analyzed the demography of *Fagus grandifolia* in Woodyard Hammock by means of matrix population models (Caswell 1989). These models were used to identify the most influential vital rates for the growth of this population, and to test hypotheses about the

mechanism responsible for the persistence of this species under frequent hurricane disturbance.

Chapter 1

Old-growth Condition in the Southern Mixed Hardwood Forest*

INTRODUCTION

The Southern Mixed Hardwood Forest, one of the southernmost mesic temperate forest types in North America, occurs along the southeastern Coastal Plain of the United States from the Carolinas to eastern Texas. These forests contain a diverse mixture of evergreen and deciduous broad-leaved trees combined with evergreen coniferous trees. Typically, they are dominated by *Fagus grandifolia* (American beech), *Magnolia grandiflora* (southern magnolia) and *Pinus* spp. (Quarterman and Keever 1962, Monk 1965, 1967, 1968, Marks and Harcombe 1975, Platt and Schwartz 1990, Vankat 1990). As the climate of the southeastern Coastal Plain, at least along the coast of the Gulf of Mexico, remained relatively constant during the Pleistocene, present mesic hardwood forests may represent relicts derived from the early Tertiary flora (Axelrod 1958,1966, Platt and Schwartz 1990). In addition, they would have served as refuge for many northern temperate species during the Pleistocene glaciations (Davis 1981, Delcourt and Delcourt 1987, Webb 1990).

Before European settlement, stands of Southern Mixed Hardwood Forest formed narrow bands of vegetation between floodplain forests and upland xeric forests or savannas dominated by *Pinus palustris* (longleaf pine). These sites were naturally protected from frequent flooding and from growing-season fires initiated in the pine savannas (Williams 1827, Delcourt and Delcourt 1974, 1977,

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Marks and Harcombe 1981, Schafale and Harcombe 1983, Platt and Schwartz 1990, Ware et al. 1993, Schwartz 1994, Harcombe et al. 1995). After European settlement virtually all pine savannas were clearcut and their characteristic growing-season fires were suppressed. Following such disruption, hardwood species and pines (especially *Pinus taeda*) replaced *P. palustris*, forming woodlands and forests that replaced most of the savannas. Stands of Southern Mixed Hardwood Forest are frequently affected by hurricanes along the Coastal Plain (Jarvinen et al. 1984, Neumann et al. 1992). These disturbances, which recur within the lifespan of most canopy trees, greatly influence the dynamics of these forests (Glitzenstein et al. 1986, Platt & Schwartz 1990).

Preservation or restoration of the Southern Mixed Hardwood Forest requires criteria for recognizing the so-called old-growth stands (Thomas et al. 1988). The concept of old growth was originally developed for Pacific Northwest forests, based on the notion that those forests undergo a directional autogenic succession toward a steady-state climax that is disrupted by natural devastations (Franklin et al. 1981, 1986, Franklin and Spies 1984). In this context old-growth condition becomes essentially synonymous with climax state. Application of the old-growth concept in other regions has tended to result in transferral of this connotation to different forests (e.g. Barnes 1989, Hayward 1991). This created difficulties for characterizing the old-growth condition of forests that, being affected by frequent disturbances (see Tyrrell 1992), may not approach a climax or a steady state (Jones 1945, Raup 1964, White 1979, Denslow 1980, Pickett and White 1985, Platt and Schwartz 1990). In these cases, an old-growth forest would be one which has not been recently cleared

and whose dynamics are essentially the same as those that historically shaped forest structure and composition ("age" and "disturbance" criteria, Hunter 1989). The old-growth definition would then contain attributes expected in a forest likely to change under a natural disturbance regime, rather than attributes expected in a steady-state community.

In this report we characterize the old-growth condition for the Southern Mixed Hardwood Forest based on published accounts and on data from five exemplary stands that show no evidence of having been cleared by man or by natural agents during the last 200 years. The two easternmost stands are located near each other, one (Woodyard Hammock) in northern Florida and the other (Titi Hammock) in southern Georgia; two central stands (Zemurray Forest and Tunica Hills) are in eastern Louisiana, and the westernmost stand (Weir Forest) is in eastern Texas (see Chapter Appendix for a detailed presentation of the exemplary forests). Structure and composition data were compiled from mapped-plot data bases and published reports related to all five forests. Description of immediate hurricane effects was based on censuses conducted after 1985 Hurricane Kate in Woodyard Hammock and Titi Hammock. Dynamics over a 14-year period were described based on an ongoing long-term study in Woodyard Hammock. This forest type was defined by Quarterman and Keever (1962) and corresponds to the Lower Slope Hardwood Pine Forest of Marks and Harcombe (1981), to forest type 66 in Vankat (1990), and partially to Southeastern Forest Experimental Station types 31, 37 46 and 59 as well as SAF types 82 and 89 (Eyre 1980).

OLD-GROWTH CHARACTERISTICS

Distribution in the landscape: Old-growth Southern Mixed Hardwood Forests are small stands whose origin predates extensive European settlement. All of the exemplary forests occupied mesic sites associated with streams or lakes. These sites are moister than the uplands and so are relatively protected from the lightning-initiated fires that frequently burned the upland pine savannas (Platt and Schwartz 1990, Harcombe et al. 1995).

Strata and growth forms: Southern Mixed Hardwood Forests have an overstory of evergreen and deciduous broad-leaved species and evergreen needle-leaved species, mostly composed of trees 20-30 m tall, and an understory of trees less than 15 m tall, usually of evergreen and deciduous broad-leaved species (Harcombe and Marks 1977, Platt 1985, Platt and Hermann 1986). Trees support lianas and sometimes fairly abundant epiphytes. Except in gaps, the ground cover of herbs is sparse, probably as a result of the abundance of evergreen trees (Marks and Harcombe 1975, Platt and Schwartz 1990).

Overall diversity:The exemplary forests averaged 37 tree species (d.b.h. ≥ 2 cm). About 28 of these species reached at least 10 cm d.b.h. (Table 1.1). The rest were large shrubs and a few species dispersed from nearby environments and present only as juveniles. Diversity index *N1* (= $e^{H'}$) indicates that about 15 of the species in each stand contributed significantly to total density, and *N2* (= *1/D*) that about 11 shared dominance (Table 1.1).

Overstory species: Dominant species of large overstory trees in the exemplary forests always included *Fagus grandifolia*, *Magnolia grandiflora*, and

Liquidambar styraciflua (sweetgum), some of the oak species *Quercus nigra* (water oak), *Q. alba* (white oak), *Q. michauxii* (swamp-chestnut oak), and, except in Tunica Hills, either *Pinus glabra* (spruce pine) or *P. taeda* (Tables 2 and 3). In each exemplary forest there were about 13 species of large overstory trees (d.b.h. ≥ 50 cm), about half of which shared dominance (respectively, *N0* and *N1*, Table 1.1). Thus, the composition of the overstory was fairly constant among the exemplary forests despite some variation in species abundance. *Fagus grandifolia* was always either the first or the second most abundant species in the overstory. An additional 30 native overstory species were represented in the exemplary forests (Table 1.2).

TABLE 1.1. Tree species diversity in five Southern Mixed Hardwood Forests. *N0* is the total number of species; $N1 = e^{H'}$, where H' is the Shannon-Wiener index, measures the number of non-rare species; and $N2 = 1/D$, where D is the Simpson index, measures the number of dominant species (see Hill 1973). All indices were calculated with overall stand tree density data.

Sizes	Range	Median	Sites
d.b.h. ≥ 2 cm			
N0	28 - 60	37	4
N1	5 - 20	15	4
N2	3 - 12	11	4
d.b.h. ≥ 10 cm			
N0	25 - 43	28	4
N1	12 - 16	14	4
N2	9 - 11	10	5
d.b.h. ≥ 50 cm			
N0	8 - 15	13	5
N1	8 - 15	7	5
N2	4 - 12	6	5

TABLE 1.2. Large and small tree presence (number of sites out of 5), density ranges, and density averages (median number of trees/ha) for common species in five old-growth Southern Mixed Hardwood Forests.

	Large trees (d.b.h. > 50 cm)			Small trees (10 cm < d.b.h. ≤ 50 cm)		
	Presence	Density range	Density median	Presence	Density range	Density median
Overstory species:						
Fagus grandifolia	5	6.0 - 18.0	9.0	5	3.0 - 102.0	38.5
Magnolia grandiflora	5	2.0 - 24.7	5.4	5	10.0 - 59.0	19.6
Liquidambar styraciflua	5	0.3 - 5.0	3.0	5	19.6 - 66.9	36.0
Quercus nigra	4	0.2 - 5.0	3.0	5	0.8 - 22.0	12.7
Quercus alba	4	0.0 - 5.0	2.0	5	1.5 - 40.5	5.0
Quercus michauxii	4	0.4 - 2.0	0.9	4	1.8 - 28.0	6.5
Liriodendron tulipifera	4	0.9 - 5.4	2.0	4	1.0 - 6.5	1.8
Nyssa sylvatica	4	0.5 - 3.5	0.8	4	13.0 - 22.4	18.9
Pinus glabra	3	4.4 - 16.5	4.4	3	10.9 - 25.4	10.9
Pinus taeda	3	1.6 - 22.0	1.6	4	0.2 - 48.0	0.4
Carya glabra	3	0.7 - 2.4	0.7	3	1.0 - 9.4	1.0
Quercus hemisphaerica	3	0.2 - 1.8	0.2	4	0.4 - 15.8	1.0
Quercus shumardii	2	0.4 - 9.0	0	2	0.9 - 6.0	0
Magnolia virginiana	1	1.4 - 1.4	0	4	0.7 - 10.6	4.0
Carya tomentosa	1	0.4 - 0.4	0	3	0.8 - 2.2	0.8
Carya cordiformis	1	1.0 - 1.0	0	2	1.0 - 8.4	0
Tilia americana	1	0.8 - 0.8	0	2	4.0 - 5.2	0
All overstory species:		40.0 - 70.0	46.0		140.0 - 275.0	227.0
Understory species:						
Ilex opaca				5	1.0 - 59.0	30.4
Carpinus caroliniana				5	1.3 - 41.0	21.1
Ostrya virginiana				4	8.0 - 69.8	27.0
Cornus florida				4	2.4 - 30.0	7.8
Acer rubrum				4	0.8 - 32.0	1.0
Symplocos tinctoria				4	0.4 - 5.5	1.0
Prunus serotina				4	0.2 - 3.0	0.4
Aralia spinosa				2	0.2 - 1.0	0
Cercis canadensis				2	0.2 - 2.4	0
Halesia diptera				2	5.0 - 8.5	0
Oxydendron arboreum				2	5.8 - 16.0	0
All understory species:					114.0 - 163.2	125.0
All species:		40.0 - 70.0	46.0		304.0 - 389.0	351.6

Additional species found in only one exemplary forest.
Overstory: *Carya illinoiensis, Castanea pumila, Celtis laevigata, Gleditsia triacanthos, Juglans nigra, Magnolia pyramidata, Paulownia tomentosa, Pinus echinata, Platanus occidentalis, Quercus falcata, Q. marilandica, Q. muehlenbergii, Q. nuttallii, Q. pagodaefolia, Q. phellos, Q. stellata, Q. virginiana, Tilia americana, Ulmus alata, U. americana.*
Understory: *Acer negundo, A. saccharum, Bumelia lanuginosa, Fraxinus americana, F. caroliniana, F. pensylvanica, Lindera benzoin, Morus rubra, Osmanthus americana, Persea borbonica, Planera aquatica, Prunus caroliniana, Sassafras albidum, Ulmus rubra, Viburnum rifidulum.*

TABLE 1.3. Basal area ranges and medians (m^2/ha) for common overstory species, for all trees, and for small and large trees in five old-growth Southern Mixed Hardwood Forests. Minimum d.b.h. of trees included in the calculation of basal area for common species and for all trees was 2 cm for Woodyard Hammock, Titi Hammock and Tunica Hills, 1 cm for Zemurray Forest, and 4.5 cm for Weir Woods.

	Basal area	Basal area
Fagus grandifolia	2.6 - 9.3	5.4
Magnolia grandiflora	1.5 - 11.6	4.0
Liquidambar styraciflua	1.1 - 4.3	3.7
Quercus nigra	0.7 - 3.2	1.9
Quercus alba	0.2 - 3.0	1.0
Quercus michauxii	0.1 - 1.1	0.9
Liriodendron tulipifera	0.4 - 2.7	0.8
Nyssa sylvatica	0.7 - 2.3	1.1
Pinus glabra	3.9 - 6.9	3.9
Pinus taeda	0.1 - 10.5	0.5
Carya glabra	0.5 - 1.8	0.5
Quercus hemisphaerica	0.3 - 1.0	0.3
Quercus shumardii	0.1 - 3.1	0.0
Magnolia virginiana	0.1 - 1.2	0.1
Carya tomentosa	0.0 - 0.5	0.0
Carya cordiformis	0.3 - 0.3	0.0
Tilia americana	0.2 - 0.6	0.0
All trees	29.0 - 40.0	33.0
Trees (d.b.h. ≥ 10 cm)	27.0 - 38.0	33.0
Trees (d.b.h. ≥ 50 cm)	12.0 - 24.0	13.0

Understory and vine species: The understory of the exemplary forests contained small individuals of overstory species and several species that never reach the overstory (Table 1.2). Among the latter, *Ilex opaca* (American holly),

Carpinus caroliniana (American hornbeam), and *Ostrya virginiana* (eastern hophornbeam) frequently shared dominance (Table 1.2). However, species abundance in the understory was variable among sites. The dominant understory species were *Ostrya virginiana* in Woodyard Hammock, *Cornus florida* (flowering dogwood) in Titi Hammock, *Halesia diptera* (two-wing silverbell) and *Illicium floridanum* (Florida anise) in Zemurray forest, *Carpinus caroliniana* in Tunica Hills and *Ilex opaca* in Weir Forest. In stands not recently affected by a hurricane, understory trees may be clumped in localized gaps (Platt and Hermann 1986). Characteristic species of lianas in the exemplary forests were *Bignonia capreolata* (cross-vine), *Decumaria barbara* (wood-vamp), *Toxicodendron radicans* (poison-ivy), *Smilax rotundifolia* (bullbrier), and *Vitis aestivalis* (summer grape); the main epiphyte was *Tillandsia usneoides* (spanish moss).

Density and Basal Area: Total basal area in the exemplary forests was similar to the 25-35 m^2/ha range reported by Parker (1989) for hardwood forests of the Central Hardwood Region (Table 1.3). However, density of trees 10 cm d.b.h. or larger ranged from 344 to 435 trees/ha (median 396 trees/ha), while the density range reported for the Central Hardwood Region was 161-427 trees/ha (Parker 1989). In addition, the median tree density in the exemplary forests exceeds the 250 trees/ha reported by Martin (1992) for a mixed mesophytic forest in Kentucky. High density in the exemplary forests resulted largely from the large number of small trees (Table 1.2). Reported density and basal area of large overstory trees (d.b.h. $\geq$ 50 cm) were extremely high in Zemurray Forest (70 trees/ha, 24 m^2/ha, White 1987). In the rest of the exemplary forests, density

TABLE 1.4. Ranges and averages (medians) of forest structural characteristics observed in Southern Mixed Hardwood Forests. [1] Percentile 95 of the age frequency distribution.

	Range	Median	Sites
d.b.h. of largest trees (cm)			
Magnolia grandiflora	72 - 126	95	5
Fagus grandifolia	77 - 98	86	5
Nyssa sylvatica	58 - 86	81	4
Pinus glabra	72 - 81	80	3
Liriodendron tulipifera	54 - 116	78	4
Pinus taeda	47 - 80	72	4
Quercus alba	48 - 82	71	4
Carya glabra	60 - 78	70	3
Quercus nigra	31 - 79	68	5
Liquidambar styraciflua	54 - 91	63	5
Quercus michauxii	39 - 74	61	5
Quercus hemisphaerica	38 - 55	54	3
Age of old trees (yrs)[1]:			
Magnolia grandiflora		214	1
Fagus grandifolia		210	1
Liquidambar styraciflua		210	1
Quercus alba		170	1
Pinus taeda		94	1
Pinus glabra		46	1
Variation in Tree Diameter:			
Number of 10cm d.b.h. classes	8 - 11	9	4
Evergreen species:			
Basal area (% of total)	7 - 52	43	5
Dead Trees:			
Standing dead (snags/ha)		10.8	1
Down logs (m^3/ha)		71.5	1

of large overstory trees ranged from 40 and 47 trees/ha and basal area from 12 to 14 m^2/ha (Table 1.2).

Size/age distributions: Few overstory trees in the exemplary stands reached 100 cm of d.b.h., but many exceeded 50 cm (Table 1.4). In the overstory of these forests, long-lived species, such as *Fagus grandifolia*, *Magnolia grandiflora* and *Liquidambar styraciflua*, were mixed with short-lived trees, such as *Pinus glabra* or *P. taeda* (Table 1.4). When all tree species were combined, density of trees in these forests decreased with tree size (Harcombe and Marks 1978, White 1987, Platt and Schwartz 1990). Populations of *Pinus* spp., however, usually had a scarcity of small size classes suggesting a single-aged condition. For long-lived dominant overstory species, small trees were scarce in some forests but not in others. For example *Magnolia grandiflora* had very few juveniles in Woodyard Hammock but many in Weir Forest (see also Harcombe and Marks 1978, Hirsh 1981, Glitzenstein et al. 1986, White 1987).

Gaps: Expanded gaps (sensu Runkle 1982) in Woodyard Hammock occupied about 30 percent of the area before Hurricane Kate. Before Hurricane Kate, small individuals of *Carya* spp. (hickories), *Quercus nigra* and *Q. michauxii* in Woodyard Hammockwere associated with old gaps (Platt and Hermann 1986). In addition, rapidly-growing, short-lived, deciduous understory species, such as *Ostrya virginiana*, *Carpinus caroliniana* and *Cornus florida* were associated with new gaps, while the slow-growing, long-lived, evergreen *Ilex opaca* and *Symplocos tinctoria* (sweetleaf) were associated with old gaps (Platt and Schwartz 1990). After Hurricane Kate, many juvenile *Pinus glabra* and *O. virginiana* reached 2 cm d.b.h. in gaps enlarged by the disturbance.

Dead component: Density of standing dead trees observed in Woodyard Hammock seven years after Hurricane Kate (11 snags/ha) was lower than the 19-44 snags/ha range reported for the Central Region Mixed Mesophytic Forest (Parker 1989). Total volume of dead wood on the forest floor in Woodyard Hammock in 1992 was probably influenced by the recent hurricane (Table 1.4). Twice as much dead wood per unit area occurred in gaps as beneath closed canopy. It took about 9 years for half of the dead trees (d.b.h. ≥ 10cm) to disappear (estimated in 1992 from presence/ absence of remains of the mapped trees that died in Woodyard Hammock between 1978 and 1990). Logs of *Pinus glabra* and *Ostrya virginiana* disappeared more slowly than logs of *Magnolia grandiflora*, *Fagus grandifolia*, *Carpinus caroliniana*, and *Ilex opaca*.

REGIONAL AND LOCAL VARIATION

Southern Mixed Hardwood Forest species composition, diversity, and proportion of evergreen and deciduous trees vary throughout the Coastal Plain. The geographical distributions of some tree species terminate or are interrupted within the Coastal Plain, presumably in relation with climatic gradients or geological history. For example, the distributions of *Pinus glabra* and *Oxydendron arboreum* do not extend west of the Mississippi River, and the distribution of *Liriodendron tulipifera* (yellow poplar) terminates in central Louisiana (Kossuth and Michael 1990, Overton 1990, Beck 1990). Before European settlement, no pines grew near the Mississippi River (Delcourt and Delcourt 1974), explaining the absence of pines in the Tunica Hills old-growth forest.

The number of evergreen species in the Southern Mixed Hardwood Forest decreases to the north while the number of deciduous species decreases to the south (Blaisdell et al. 1974, Greller 1980, Ware et al. 1993). The northernmost limit of *Magnolia grandiflora* occurs at the southeastern corner of North Carolina (see Ware et al 1993, Ware 1970). This limit has been proposed to be associated with seed and seedling sensitivity to freezing (Evans 1933). *Fagus grandifolia* and *Quercus alba* do not grow in southeastern Georgia and the peninsula of Florida (Ward 1967). Ranges of the other temperate tree species terminate progressively from north to south along the central ridge of the peninsula of Florida, and very little mixing occurs with tropical tree species. As a result, tree species diversity in temperate hardwood forests decreases along the peninsula (Greller 1980, Schwartz 1988, Platt and Schwartz 1990). Diversity of epiphytes and ferns, however, increases in this direction by the addition of tropical species (Schwartz 1988, Platt and Schwartz 1990). In mesic hardwood forests of northern Florida, less than one third of the overstory species are evergreen, but farther south in the peninsula evergreens are more than half of the overstory species (Greller 1980). Located west of the Florida peninsula, the exemplary forests contained less than one third evergreen species in the overstory, but the basal area of these evergreen species was 43-52% (Table 1.4) of total basal area of overstory species (except in the Tunica Hills where it was 7%).

Southern Mixed Hardwood Forest old-growth composition varies with local soil conditions and subtle topographic gradients. In Northern Florida, Monk (1965) found that the proportion of evergreen trees in hardwood forests was

highest on dry sterile soils, and that maximum community diversity occurred on mesic calcareous soils. In ordination analyses of the original 30 quantitative censuses from Quarterman and Keever (1962), Ware (1978, 1988) found that higher abundance of *Quercus hemisphaerica* (laurel oak) and lower of *Fagus grandifolia* were apparently associated with relatively low moisture and coarse soil texture. In Eastern Texas, Marks and Harcombe (1981) found that species composition varied with changes of soil texture over the landscape. Their Lower Slope Hardwood Pine forest, which had the maximum proportion of evergreen species, occurred in the middle of the soil texture gradient. In northwest Florida, Gibson (1992) found that topography accounted for the main compositional differences within a forest dominated by *Q. hemisphaerica*.

Both Platt and Schwartz (1990) and Harcombe et al. (1995) suggested that fire occurrence interacts with edaphic factors and topography to determine the distribution of hardwood forest tree species. According to Platt and Schwartz (1990), low-intensity, growing-season fires on the uplands may prevent some species from mesic and hydric forests, such as *Liquidambar styraciflua*, *Quercus nigra*, *Pinus taeda*, and *Carpinus caroliniana*, from invading up-slope. A similar situation was proposed for the Kisatchie National Forest in western Louisiana, where fire was hypothesized to play a key role in determining the differences between mesic stands, dominated by *Fagus grandifolia*, *Magnolia grandiflora*, *Quercus michauxii*, *Q. alba*, and *Q. nigra*, and drier stands dominated by *Quercus stellata*, *Q. marilandica*, *Q. falcata*, *Q. velutina*, *Q. alba*, *Carya* spp., *Pinus echinata* (shortleaf pine), and *P. taeda* (Martin and Smith 1991).

OLD-GROWTH DYNAMICS

Tree recruitment, growth, and mortality in old-growth Southern Mixed Hardwood Forests do not seem to have occurred at steady annual rates. Instead, these processes would have had pulses as a result of natural disturbances (Harcombe and Marks 1978, Glitzenstein et al. 1986, Platt and Schwartz 1990). In the past, creeping fires that started in the uplands might have frequently killed seedling and understory trees and damaged adult trees (especially *Fagus grandifolia*, see Blaisdell et al 1974). In contrast, crown or devastating fires have not been recorded in these forests. In Woodyard Hammock, a summer drought in 1981 killed many small trees and slowed tree growth rate. Intermittent streams, changing their course across the forest, have also caused localized tree mortality in Woodyard Hammock.

The most conspicuous disturbances affecting Southern Mixed Hardwood Forests are hurricanes. All of the exemplary forests were exposed to four to six storms with winds over 100 km/h between 1886 and 1992 (Table 1.5). In 1985, Hurricane Kate passed near Woodyard Hammock and Titi Hammock with winds of about 160 km/h. In Woodyard Hammock, this storm extensively disrupted the canopy: expanded gaps (sensu Runkle 1982) were increased from 31% to 62% of the area, and 58% of large hardwood trees and 80% of large pines were damaged. However, tree mortality was low, 98% of all hardwoods, 95% of large (d.b.h. $\geq$ 45 cm) hardwoods, 65 % of all pines and 61% of large pines survived. The effect of Hurricane Kate on species diversity was minor; the number of common species (measured as $N1 = e^{H'}$) was 12.0 in 1984 and 11.7 in 1986. In Titi Hammock, the patterns of tree damage and mortality were similar. None of

the hurricanes recorded near the exemplary forests between 1886 and 1992 greatly exceeded the intensity of Hurricane Kate (Jarvinen et al. 1984). Hence, none of these forests has undergone a hurricane of the magnitude of Camille (1969) or Hugo (1991). Such major hurricanes are, however, very unlikely to impact on these forests because they have a low frequency of landfall along the Gulf of Mexico coastline.

TABLE 1.5. Dates at which storms occurred with maximum sustained winds of more than 100 km/h within 100 km of each of the exemplary forests between 1886 and 1992. Data obtained from NOAA records (Jarvinen et al. 1984).

Sites	Dates of storms
Woodyard Hammock, FL.	June 1886, October 1894, October 1941, November 1985.
Titi Hammock, GA.	June 1886, October 1894, October 1941, November 1985.
Zemurray Forest, LA.	August 1893, September 1909, September 1920, September 1945, September 1985.
Tunica Hills, LA.	August 1888, September 1909, September 1920, August 1926, September 1947, August 1992.
Weir Forest, TX.	October 1886, July 1891, August 1940, June 1986

In Woodyard Hammock, disruption of the canopy by Hurricane Kate prompted marked changes in tree recruitment, growth and mortality in

subsequent years. Before the disturbance, recruitment rates were low, and thinning of juveniles and small trees was intense. Tree mortality decreased with increasing size, and large tree mortality was very low. Average growth rates of large trees were high, and juveniles were almost completely suppressed (Table 1.6). As a result, total density was decreasing, and basal area was becoming increasingly concentrated in large trees. After the hurricane, there was a

TABLE 1.6. Average rates of recruitment, tree growth, and mortality observed in Woodyard Hammock during periods before (1978-84), including (1984-86) and after (1986-92) Hurricane Kate. Standard errors shown in parentheses. Juveniles (2cm≤d.b.h.<10cm); Small trees (10cm≤d.b.h.<50cm); Large trees (50cm≤d.b.h.).

	1978-84	1984-86	1986-92
Recruitment (trees/ha/yr)	13.8	43.3	81.0
Annual growth (mm/yr)			
Juveniles	0.66 (.02)	1.27 (.04)	1.61 (.03)
Small trees	1.90 (.05)	1.30 (.04)	1.94 (.06)
Large trees	4.07 (.19)	1.64 (.15)	1.96 (.16)
Annual mortality (%)			
Juveniles	5.58 (.21)	5.31 (.38)	3.41 (.15)
Small trees	2.58 (.15)	4.04 (.33)	1.98 (.14)
Large trees	0.71 (.23)	4.73 (.99)	2.03 (.39)

massive recruitment into the juvenile size class (d.b.h. ≥ 2 cm), which mostly resulted from release of small individuals present at the time of the storm. Juvenile mortality decreased and juvenile annual growth rate more than doubled (Table 1.6). Mortality of large trees increased greatly, and large-tree annual growth rate was halved (Table 1.6). As the result, total tree density (d.b.h. ≥ 2 cm) increased 36% in 6 years, even though total tree basal area remained stable. As most of the new recruits were *Pinus glabra* or *Ostrya virginiana*, forest species composition (d.b.h. ≥ 2 cm) changed rapidly in the years that followed Hurricane Kate. In contrast, the rate of change in species composition of trees more than 10 cm declined from the pre- to the post-hurricane period, mainly because ongoing thinning of suppressed *P. glabra* and *Carpinus caroliniana* ceased.

THE NATURE OF OLD GROWTH

The Southern Mixed Hardwood Forest was presented by Quarterman and Keever (1962) as the "climatic climax" in the Southeastern Coastal Plain, as part of a long tradition of assigning climax status to the mesic hardwood forests of the region (Gano 1917, MacGowan 1937, Kurz 1944, Braun 1950, Monk 1965, 1967, 1868, Delcourt and Delcourt 1974,1977, Blaisdell et al. 1974, Ware et al. 1993). The main basis for this argument has been that fire suppression in the upland pine-savannas is followed by hardwood encroachment. This concept was based on the assumption that Southern Mixed Hardwood Forests were essentially equilibrium forests that resulted from a directional autogenic succession (Quarterman 1981). However, this concept gave little consideration

to hurricanes that frequently impact the Coastal Plain (Neumann et al. 1992, Jarvinen et al. 1984). These disturbances constitute a strong allogenic influence that may prevent these forests from approaching an equilibrium (Glitzenstein et al 1986, Platt and Schwartz 1990).

The hurricane regime affecting the Southern Mixed Hardwood Forest is characterized by high frequency (several per century) of storms that, while extensively damaging the canopy, result in low tree mortality. In contrast, complete forest devastation by natural agents, such as very intense hurricanes or crown fires, appears to be extremely rare. In each site, recurrence time of hurricanes may be highly variable, and patterns of hurricane damage may vary among storms (Platt et al. in prep.). Frequent, non-devastating hurricanes would account for the larger proportion of the area occupied by gaps, lower density of standing dead trees, and relatively smaller sizes of canopy trees than in northern temperate old-growth forests (see Quigley and Platt 1995). High tree density would occur because mortality of suppressed trees is likely to be interrupted by a disturbance. Repeated canopy disruption, with the consequent increases in light in the understory, would account for high rates of recruitment and growth.

Hurricanes can be followed by waves of tree recruitment, growth, and death resulting in changes in the density and structure of tree populations and in consequent fluctuations in forest species composition. Under a regime of frequent low-intensity hurricanes, stands of Southern Mixed Hardwood Forest are not likely to reach an equilibrium structure and composition. Regeneration in periodic canopy openings would prevent the long-lived shade tolerant canopy

trees from displacing the short-lived, shade-intolerant pines and the small-statured understory species. However, the non-devastating nature of such disturbances also results in shade-tolerant species surviving frequent disruptions (Connell 1978). In addition, since hurricanes may disrupt large proportions of the canopy, changes occurring in disturbed patches are likely to be reflected throughout the stand (Smith and Urban 1988, O'Neill et al. 1986). The classical interpretation of these effects of frequent, non-devastating disturbances, consistent with the directional succession model, is that disturbances produce a retrogression to pre-climax seral stages followed by a new autogenic succession toward the climax (see MacGowan 1937). However, because hurricanes often occur at intervals shorter than the lifespan of trees, and because their immediate effects can be variable; successional tendencies due to tolerance and competitive displacement would be minor compared to the processes of regeneration and change that result from the timing and immediate effects of the disturbances (Platt and Schwartz 1990). One strong suggestion against the retrogression notion is that *Pinus glabra*, a light-demanding species that is recruited into the canopy in gaps enlarged by the hurricanes, does not behave as a pioneer, but instead is endemic to these old-growth forests. As the climate of the Southeastern Coastal Plain along the Gulf of Mexico coastline remained relatively unchanged during the Pleistocene, chronic disturbance to these forests may have selected traits in the life-history of the tree species that make them adapted for, or even dependent on, the disturbance (Denslow 1980, Platt and Schwartz 1990).

Disturbances affecting the Southern Mixed Hardwood Forest appear to be critical for both regeneration and change in old-growth stands. Allogenic disturbances would have been necessary for recruitment or growth of many of the tree species into the canopy of these forests and, therefore, for their continued coexistence. Wide variation in the frequency of disturbances and probably in their immediate effects would have determined changes in stand structure and composition. As complete stand devastation by natural agents was probably very rare in this forest type, old-growth stands may have existed for many generations of trees under the effects of frequent, non-devastating disturbances. Regeneration and change associated with these disturbances, rather than the hypothesized directional succession (Quarterman and Keever 1962, Bormann and Likens 1979, Quarterman 1981), are likely to have dominated the natural dynamics of these forests over most of their history.

APPENDIX: EXEMPLARY FORESTS

Woodyard Hammock is a 30-ha hardwood forest located 32 km north of Tallahassee, Leon County, in northern Florida (30°35'N, 84°20'W). It occupies flat terrain along the northern shore of Lake Iamonia. Part of an antebellum plantation established in the early 1800's, it has been managed as a part of Tall Timbers Research Station since 1959 (Blaisdell et al. 1974, Hirsh 1981, Platt and Hermann 1986, Platt and Schwartz 1990). According to records of the National Oceanic and Atmospheric Administration (NOAA, Neumann et al. 1992), between 1886 and 1992 four hurricanes with winds over 100 km/h , in 1886, 1894, 1941, and 1985 (Hurricane Kate), passed within 100 km of Woodyard Hammock. Even though creeping fires originating in surrounding

pine-land entered the forest in the past, this has not happened recently, at least since 1959 (Hirsh 1981). During the early 1900's, dead trees were salvaged for firewood and some large *Pinus taeda* (loblolly pine) were cut. In 1978, a 4.5-ha permanent study plot was established in the middle of Woodyard Hammock (Hirsh 1981, Platt and Hermann 1986). All trees in the plot 2 cm d.b.h. or larger were measured, mapped, and tagged. Censuses were repeated biennially to record tree recruitment, growth, and death. Gaps were periodically mapped as polygons formed by connecting the bases of their bordering canopy trees (expanded gaps, Runkle 1982). After Hurricane Kate in 1985, damage to each mapped tree was assessed. Trees that died between 1978 and 1990 and extant dead material were sampled in 1992 to estimate density of snags, volume of downed logs, and rates of disappearance.

Titi Hammock is a 117-ha hardwood forest located in Thomas County, in southern Georgia, 14 km south of Thomasville (30°41'N, 84°00'W). It is part of Springhill Plantation, established in the early 1800's, and is currently preserved by The Nature Conservancy. This forest occupies steep terrain with a 20-m change in elevation along the bluffs of Titi Creek. Along the slope, three different plant associations can be distinguished (Platt 1985). In the past, dead trees were salvaged for firewood and some large pines may have been selectively cut on the upper slope. A creeping fire entered the forest in 1968 (Blaisdell et al. 1974). The site is near Woodyard Hammock and was exposed to the same hurricanes as that forest. A 5-ha permanent study plot was established in Titi Hammock in 1985 before Hurricane Kate. All trees in the plot 2 cm d.b.h. or larger were tagged, measured, and mapped. Damage to mapped trees by

Hurricane Kate was assessed in 1986, and in 1990 the whole plot was surveyed for tree growth and survival.

Zemurray Forest is a 35-ha hardwood forest located in Tangipahoa Parish, in eastern Louisiana, 80 km north of New Orleans (30°37'N, 90°21'W). It occupies a level site with acid soil, in the floodplain of Chappepeela Creek (White 1987). According to NOAA records (Jarvinen et al. 1984), between 1886 and 1992 four hurricanes have passed within 100 km of this location with wind of more than 100 km/h. Quarterman and Keever (1962) included this forest in their extensive survey of the Southern Mixed Hardwood Forest. We used detailed information on structure and composition of this forest, obtained by White (1987), based on the analysis of ten 0.2-ha plots.

Tunica Hills is a forest tract located in West Feliciana Parish, in eastern Louisiana, 60 km northwest of Baton Rouge and 2 km east of the Mississippi River (30°47'N, 91°29'W). It has second-growth pine forest on the uplands and old-growth hardwood forest on steep ravine slopes (Delcourt and Delcourt 1974). The forest is being managed as a preserve by The Nature Conservancy. According to NOAA records (Jarvinen et al. 1984), between 1886 and 1992 six hurricanes with winds more than 100 km/h passed within 100 km of this site. We used data obtained by Quigley (1994) who measured, tagged, and mapped all trees 1 cm d.b.h. or greater in 16 randomly located hardwood plots of 1/16 ha each.

Weir Forest is located 16 km north of Beaumont, in Hardin County, in eastern Texas, (30°16'N, 94°12'W). It occupies gently sloping terrain, slightly dissected by intermittent streams near the Neches River (Harcombe and Marks

1977). According to Glitzenstein et al. (1986), this forest was not directly affecteded by humans before the late 1800's. Around 1917, pines were selectively logged. According to NOAA records (Jarvinen et al. 1984), four hurricanes with winds more than 100 km/h passed within 100 km of this forest. A 3.2-ha plot in Weir Woods has been mapped and monitored since 1980. Data on species composition and tree sizes were provided by J. Glitzenstein and P. Harcombe. Additional information was taken from detailed analyses of structure and dynamics of this forest (Harcombe and Marks 1978, Glitzenstein et al. 1986).

Chapter 2

Alternative Responses to Hurricane Disturbance in an Old-growth Southern Mixed Hardwood Forest

INTRODUCTION

In coastal regions of eastern North America, forests are affected by hurricanes that originate in the north Atlantic Ocean. Among these forests are the Southern Mixed Hardwood Forests, a mesic temperate type that occurs in the Coastal Plain from the Carolinas to eastern Texas (Quarterman and Keever 1962). The overstory of these forests contains a diverse mixture of evergreen and deciduous broad-leaved trees (hardwoods) such as *Fagus grandifolia*, *Magnolia grandiflora*, *Liquidambar styraciflua*, *Quercus* spp., *Carya* spp., and *Nyssa sylvatica*, combined with evergreen, needle-leaved trees (pines) such as *Pinus glabra* and *P. taeda*. The understory contains small individuals of overstory species and a set of small-stature species that rarely reach the canopy, such as *Ilex opaca*, *Carpinus caroliniana*, and *Ostrya virginiana* (Quarterman and Keever 1962, Monk 1967, Christensen 1988, Marks and Harcombe 1975, Platt and Schwartz 1990, Vankat 1990, etc.). Stands of Southern Mixed Hardwood Forest located along the Coastal Plain of the northern Gulf of Mexico have been exposed, between 1886 and 1992, to four to six tropical storms with winds between 100 and 200 km/h. More intense hurricanes, however, have affected individual stands of this forest type less than once per century (Neumann et al. 1992, Batista and Platt 1996).

Hurricanes affecting Southern Mixed Hardwood Forests produced low initial mortality but extensive disruption of the canopy. As a result of canopy

disruption, the area in gaps was enlarged and light levels under the remaining canopy increased. As a consequence, formerly suppressed trees had increased growth rate, and there was increased tree regeneration, either from advance recruits or from new seedlings or sprouts (Platt and Schwartz 1990, Bill and Harcombe 1994, Batista and Platt 1996, Platt et al. in revision). In recent conceptual models, chronic disturbance by hurricanes has been proposed to have a major role in maintaining the diversity and driving the dynamics of these Southern Mixed Hardwood Forests (Harcombe and Marks 1978, Glitzenstein et al. 1986, Platt and Schwartz 1990, Batista and Platt 1996). However, observed effects of hurricanes on the dynamics the Southern Mixed Hardwood Forest have not yet been reported in detail (Bill and Harcombe 1994, Batista and Platt 1996).

By disrupting the canopy, hurricanes are likely to favor tree species that respond to increased light availability with rapid regeneration or increased growth of surviving understory individuals (cf. Grime 1977, Oliver and Stephens 1977, Connell 1978, Solbrig 1980, Canham and Marks 1985, Glitzenstein et al. 1986, Platt and Schwartz 1990). On an evolutionary time scale, disturbances that disrupt the canopy have been proposed to select for traits that result in rapid capture of their "characteristic" gaps (Denslow 1980, 1984, Stearns and Crandall 1981). However, the importance of response to canopy disruption is likely to depend on the proportion of canopy opening, which in turn is influenced by the intensity of the storm and the resistance of the canopy trees. Chronic hurricane disturbance could also select for resistance traits resulting in reduced damage and increased survival of trees (Canham and Marks 1985, Pickett and White 1985). Indeed, evidence from demographic analyses of trees suggests

that selection pressures are often stronger on survival than on growth and regeneration (cf. Silvertown et al. 1993, Batista et al. in review). Advent of adaptations resulting in increased resistance to disturbances would alter the characteristic spatial and temporal pattern of gaps created. As a consequence, these adaptations would modify the nature of selection pressures acting on traits associated with response to canopy disruption. Therefore, the relative importance of life-history strategies based on response to disturbance or on resistance to disturbance would be strongly influenced by the particular disturbance regime and by the evolutionary history of the available tree species.

In this article we report a case study of the dynamics of Woodyard Hammock, a hurricane-frequented old-growth Southern Mixed Hardwood Forest in northern Florida. We described changes in tree recruitment, growth, and mortality occurred after this forest was affected by Hurricane Kate in November 1985. Our analysis was done at the level of forest stand, based on data from periodic censuses conducted over the period spanning seven years before and seven years after the disturbance (1978 - 1992). Our objectives were to delineate the role of hurricanes in determining rates and rhythms of tree regeneration, growth, and mortality, and to assess the relative importance of response and resistance to disturbance in the persistence and abundance of tree species.

METHODS

Study site

Woodyard Hammock is a 30 ha forest located 32 km north of Tallahassee, along the northern shore of Lake Iamonia in Leon County, northern Florida (30°35'N, 84°20'W). Part of a plantation established in the

early 1800's, this forest has been managed by Tall Timbers Research Station since 1959 (Hirsh 1981). In the past, Woodyard Hammock was affected by creeping fires that originated in surrounding pine-lands, but this has not happened at least since 1959 (Hirsh 1981). During the early 1900's, trees that died in the forest were salvaged for firewood, and some large *Pinus taeda* were cut. According to records from two nearby weather stations (Quincy and Monticello, Florida), Woodyard Hammock has mean annual temperature of 19 ^{0}C, with a maximum monthly mean of 27 ^{0}C in July and a minimum of 11 ^{0}C in January; and mean annual rainfall of 1420 mm, with a minimum monthly mean of 70 mm in October and November (NOAA 1982). The growing season is about 273 days long, from March through November (Canham et al. 1990).

According to NOAA records (Jarvinen et al. 1984), between 1886 and 1992, Woodyard Hammock has been within 100 km of four storms with maximum sustained windspeeds over 100 km/h (in 1886,1894,1941, and 1985). The eye of Hurricane Kate, the last of these storms, passed within 30 km of Woodyard Hammock on November 21, 1985, following a period of heavy rainfall that had saturated the soil. During this hurricane, gusts of wind up to 160 km/h were recorded in Leon County and tropical storm force winds lasted for about eight hours (Clark 1986). Data on the hurricanes that affected five Southern Mixed Hardwood Forest stands along the coastal plain of the northern Gulf of Mexico suggest that storms substantially more intense than Hurricane Kate (e.g. Camille in 1969) have been rare in this region (Batista and Platt 1996). Climatograms (Walter 1971), constructed with data from Quincy and Monticello, Florida, suggest that Woodyard Hammock was exposed to similar patterns of

monthly rainfall and mean temperature in the seven year periods that preceded and that followed Hurricane Kate.

Field data

A 4.5 ha (225 x 200 m) permanent study plot was established in 1978 in the middle of Woodyard Hammock (Hirsh 1981; Platt and Hermann 1986). Within the plot, the greatest difference in elevation was 2.7 m. All trees in the plot with diameter at 1.5 m height (dbh) ≥ 2 cm were tagged, located in a plot map, measured for dbh, and classified as understory (≤15 m tall) or overstory (>15 m tall). Trees in the overstory stratum were further classified as subcanopy (15-20 m tall, crowns partially shaded by neighbor trees) or canopy (>20 m tall, crowns not shaded by other trees). The entire plot was censused biennially to record dbh growth and recruitment of trees. Stems that grew into the dbh ≥ 2 cm size class were recorded as recruits, tagged, and mapped. Mortality was recorded annually until 1985 and biennially starting in 1986. After Hurricane Kate in 1985, damage to each mapped tree was assessed. Trees that were not leaning and had no branches with diameter > 5 cm broken were classified as without major damage. The remaining trees were assigned to various categories of major damage (Platt et al. in review). The information obtained was organized in a data base containing records of 7,149 trees found in the plot in at least one of the 8 biennial censuses conducted between 1978 and 1992.

Gaps, defined as openings in the overstory, were periodically mapped as polygons formed by connecting the bases of the bordering canopy trees (i.e. the expanded gaps of Runkle 1982). These expanded gaps occupied 31% of the plot before, and 62% after Hurricane Kate (Batista and Platt 1996). In 1992, the gap area was still larger than before the hurricane, in part as a consequence of

delayed mortality of damaged canopy trees. However, a substantial proportion of the gaps were occupied by understory trees (Peters and Platt 1996).

Analysis

Forest structure and species composition.- For each tree species, we compiled the total basal area and the density in the overstory and understory strata in 1978 and 1992. Species were designated as overstory if they had any canopy individuals in the initial census and as understory otherwise. To estimate densities in the over- and the understory strata in 1992, trees were assigned to either stratum based on logistic regression models (Agresti 1990) relating stratum and dbh in 1978 for each species, and on their damage by Hurricane Kate. Each tree was assigned to the overstory if the probability of being in this stratum, as predicted by the corresponding logistic regression model given its 1992 dbh, was > 0.5 and if field records of damage indicated that, after the hurricane, it had branches with diameter > 5 cm left above 15 m height. Otherwise it was assigned to the understory stratum. This information was used to construct dominance-diversity curves (Whittaker 1965) based on total basal area and on density per stratum. Based on the dominance-diversity curves, overstory and understory species were characterized as dominant, subdominant or rare.

Recruitment.- For each species, we compiled the number of individuals that reached 2 cm dbh during the pre-hurricane (1978-84) and post-hurricane (1986-92) intervals. Individuals entering this size class between 1984 and 1986 were not included in the analysis because they could not be unequivocally assigned to either the pre- or the post hurricane recruitment. For each species,

we used the Pearson chi-square statistic (Agresti 1990) to test the hypothesis of equal number of recruits between intervals.

Growth.- Individual tree dbh increments between 1978 and 1984, and between 1986 and 1992, were compiled for all trees recorded alive at the beginning and at the end of either interval. Two types of ANOVA with repeated measurements were used to examine the patterns of growth change. First, growth was compared among trees classified by species group (pines, overstory hardwood species, understory species) and stratum (overstory and understory), and between pre-hurricane and post-hurricane periods, using initial dbh as covariate. Second, growth was separately compared between the pre- and the post-hurricane periods for each of the dominant and subdominant species in three size related classes: saplings (trees 2-4 cm dbh), understory trees with dbh≥4 cm, and overstory trees. In both types of ANOVA, we allowed for non-null covariances between pre- and post-hurricane growth because part of the measurements were obtained from the same trees in both periods and thus were not independent. In addition, we allowed for heteroscedasticity among combinations of species group by stratum by period. We used the iterative algorithm provided by SAS Proc MIXED (SAS Institute Inc. 1996) to estimate the parameters of these models by restricted maximum likelihood (Wolfinger 1993). Confidence intervals for the adjusted means obtained from these analyses were used to describe patterns of differences among species and between strata within each period. In addition, *t*-tests with paired observations were used to compare between pre- and post-hurricane growth of overstory trees of each dominant and subdominant species that survived

between 1978 and 1992 within groups with and without evident hurricane damage.

Mortality.- Pre-hurricane mortality rates were estimated using the proportions of trees alive in the 1978 census that died before the 1984 census; and post-hurricane mortality was estimated using the proportions of trees alive in the 1986 census that died before the 1992 census. The proportion of trees, alive in the 1985 mortality census (completed one week before the hurricane), that were damaged by the hurricane and died before the 1986 census was designated as direct hurricane mortality. Three separate logistic regression models (Agresti 1990) were fitted to pre-hurricane, post-hurricane, and direct hurricane mortality, using species group (pines, overstory hardwood species, understory species), stratum (overstory, understory) and initial dbh as predictors. In addition, logistic regression models were used, within the pre- and post-hurricane periods, to compare mortality among species within size classes, and to perform a-posteriori comparisons among subgroups of species. Logistic regression models were estimated by maximum likelihood using SAS Proc CATMOD (SAS Institute Inc. 1989).

Mortalities of saplings (trees 2-4 cm dbh), understory trees with dbh≥4 cm, and overstory trees in the pre- and the post-hurricane periods were compiled for the dominant overstory and understory, and for the subdominant overstory species. To test the hypothesis that trees alive in 1978 had equal probability of death in the pre-hurricane (1978-85) and post-hurricane (1985-92) intervals, we constructed a likelihood ratio test based on the multinomial distribution. This test was run separately for each dominant or subdominant species in the overstory and understory strata (dbh ≥ 4 cm) whenever the

expected numbers of dead and survivors under the null hypothesis was at least five in each period. As most of the 1978 saplings were not among the 1986 saplings, differences between pre- and post-hurricane sapling mortalities for each species were tested, assuming independence, with logistic regression (Agresti 1990).

RESULTS

Forest structure and composition

Between 1978 and 1992, 38 tree species had individuals > 2 cm dbh in the Woodyard Hammock plot. Among these, 18 species had canopy trees and were therefore designated as overstory species. The remaining 20 species only had understory or subcanopy individuals and therefore were designated as understory species (Table 2.1).

In 1978, each of the five dominant overstory species had basal area > 2 m^2/ha and density > 10 overstory trees/ha (Table 2.1). Together, these species accounted for 77% of the total basal area and 83% of the density of overstory trees (Figure 2.1). The five subdominant overstory species, had individual basal area between 0.2 and 1 m^2/ha and overstory density between 2.5 and 6 trees/ha (Table 2.1). These subdominant species accounted for 8% of the total basal area and 11% of the overstory tree density. Eight additional overstory species, designated as rare, had individual basal area < 0.2 m^2/ha and density in the overstory < 1 tree/ha (Table 2.1).

Overstory species were also abundant in the understory stratum. In 1978, three of the dominant or subdominant overstory species (*Fagus grandifolia*, *Liquidambar styraciflua*, *Quercus michauxii*), had more than 80 understory trees/ha, and accounted for 35% of the understory tree density;

Table 2.1. Basal area and density in the over- and understory strata of Woodyard Hammock in 1978 and 1992. Tree strata were recorded in the field in 1978. In 1992, trees were assigned to eitherstratum based on logistic regression models relating stratum with dbh for each species and on field notes of damage produced by Hurricane Kate.

	1978				1992			
	b.a.	density			b.a.	density		
	(m^2)	sapl.	und.	over.	(m^2)	sapl.	und.	over.
Overstory species								
Dominant:								
Magnolia grandiflora	50.9	10	60	219	44.4	12	43	188
Fagus grandifolia	24.0	140	331	104	23.4	85	361	100
Liquidambar styraciflua	18.6	19	366	172	19.4	69	190	164
Pinus glabra	16.9		57	123	9.9	377	67	53
Nyssa sylvatica	9.7		51	64	10.4	1	31	66
Subdominant:								
Quercus michauxii	4.7	82	320	22	6.0	40	222	28
Quercus nigra	3.2	16	84	26	2.8	39	38	25
Carya glabra	2.2	32	13	12	1.9	33	17	9
Liriodendron tulipifera	1.7		3	14	1.6			10
Carya cordiformis	1.3	11	58	15	1.7	2	28	15
Rare:								
Quercus virginiana	0.8			2	0.8			2
Quercus alba	0.8	1	5	4	0.4		6	3
Quercus shumardii	0.5		6	4	0.6		1	4
Ulmus alata	0.4	7	4	2	0.6	5	9	2
Pinus taeda	0.2			3	0.1			1
Quercus hemisphaerica	0.1		6	1	0.2	3	2	1
Magnolia virginiana	0.1	1	6	1	0.1		1	1
Subtotal	136.1	319	1370	788	124.3	666	1016	672

Table cond.

Understory species								
Dominant:								
Ilex opaca	7.0	116	381	17	6.5	118	348	9
Carpinus caroliniana	5.6	164	439	7	2.1	297	260	
Ostrya virginiana	4.9	63	335	9	4.3	988	358	2
Subdominant:								
Oxydendron arboreum	1.1	5	67	1	0.6	12	24	2
Cornus florida	0.6	30	112		0.4	69	61	
Acer rubrum	0.3	20	43		0.4	14	40	1
Symplocos tinctoria	0.1	89	24		0.1	89	13	
Rare:								
Morus rubra	0.1	13	6		0.0	8	12	
Prunus serotina	0.1		6		0.1	11	4	1
Osmanthus americanus	0.1	13	14		0.0	13	11	
Fraxinus pensylvanica	0.0	9	6		0.0	20	2	
Cercis canadensis	0.0		1		0.0	1		
Cyrilla recemiflora	0.0	2	3		0.0	6	6	
Quercus stellata	0.0		1		0.0		1	
Sambucus canadensis					0.0	15	3	
Rhus copollina					0.0	1		
Callicarpa americana					0.0	4		
Aralia spinosa					0.1	84	20	
Ilex coriacea					0.0	1		
Cornus foemina					0.0	1		
Subtotal	19.9	524	1438	34	14.8	1752	1163	15
Total	156.0	843	2808	822	139.1	2418	2179	687

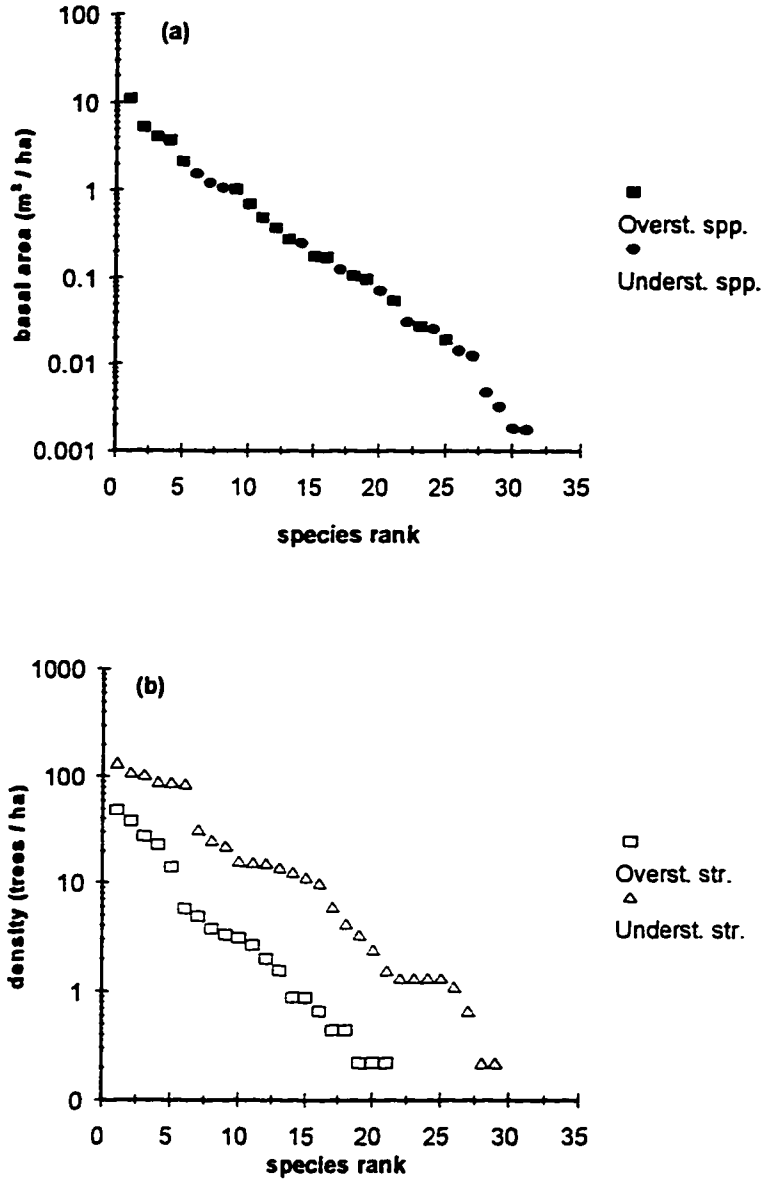

FIGURE 2.1. Dominance-diversity curves for tree species in a 4.5 ha plot in Woodyard Hammock in 1978. (a) species ranked by total basal area, black squares correspond to overstory and empty circles to understory species, (b) species ranked by density in the overstory (empty squares) and understory (triangles) strata.

while the remaining dominant or subdominant overstory species, except *Liriodendron tulipifera*, had more than 10 understory trees/ha (Table 2.1). In the sapling compartment (trees 2-4 cm dbh) only three overstory species (*F.grandifolia*, *Q. michauxii*, *Carya glabra*) were abundant. Each of these species had more than 30 saplings in the plot (7/ha). Saplings of *Pinus glabra*, *Nyssa sylvatica*, and *L. tulipifera* were absent in the plot (Table 2.1). In fact, all mapped *P. glabra* (dbh > 2 cm) were > 10 cm dbh, and all but two mapped *L. tulipifera* were > 20 cm dbh.

In 1978, 15 understory species had trees > 2 cm dbh. Three of these understory species, designated as dominant understory species, had basal area > 0.2 m^2/ha, and more than 80 trees/ha (Table 2.1), and accounted for 11% of the total basal area and 41% of the understory tree density (Figure 2.1b). Four subdominant understory species had densities between 10 and 30 trees/ha (Table 2.1), and accounted for 11% of the understory density. All remaining understory species recorded in the initial census had density < 7 trees/ha, and were designated as rare understory species (Table 2.1). The three dominant (*I. opaca*, *C. caroliniana*, *O. virginiana*), and two subdominant understory species (*C. florida*, *S. tinctoria*) were abundant in the sapling compartment (Table 2.1).

Between 1978 and 1992, total tree density in the Woodyard Hammock plot increased and total basal area slightly decreased (Table 2.1). The increase in density resulted from abundant recruitment into the smallest size classes after the hurricane. In 1992, the density of understory trees (dbh ≥ 2 cm) had increased to 1022/ha. In contrast, density of overstory trees and total basal area decreased to 153 overstory trees/ha and 30.9 m^2/ha respectively. Changes in species composition and dominance over the 1978-92 interval were also

relatively small (Table 2.1). In the overstory, the proportion of *Pinus glabra* in the overstory declined. However, the largest changes affected the sapling compartment; individuals of five species present as small shrubs before the hurricane grew into the dbh ≥ 2 cm class, and the proportion of *P. glabra* and *Ostrya virginiana* increased greately (Table 2.1).

Recruitment

In the pre-hurricane period (1978-84), mean rate of recruitment into the dbh ≥ 2 cm class was 12.4 recruits.ha^{-1}.yr^{-1}. Most trees (82%) that grew into the dbh ≥ 2 cm class were from understory species (Figure 2.2). Those understory

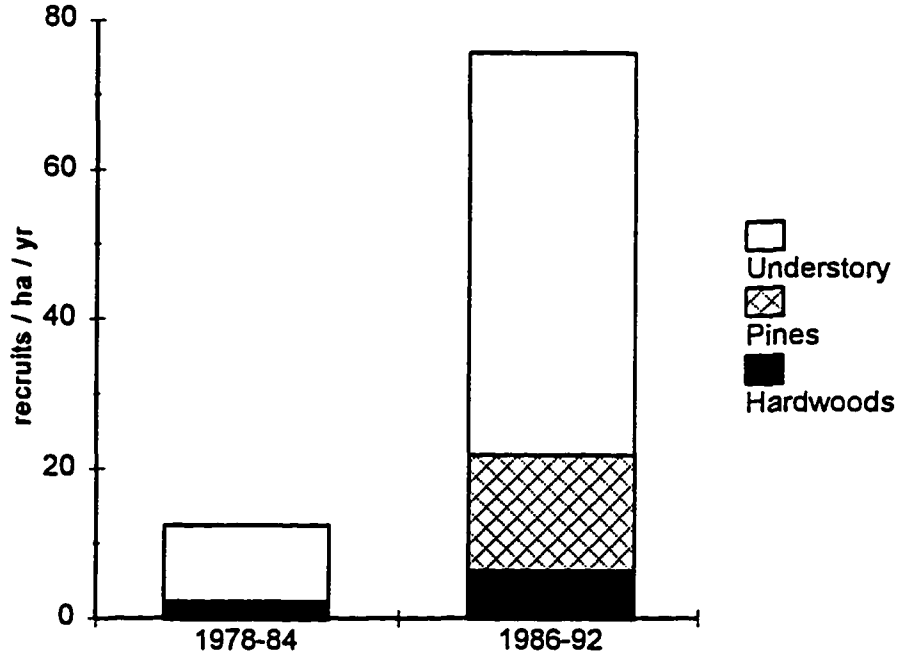

Figure 2.2. Total recruitment of trees into the dbh ≥ 2 cm size class in a 4.5 ha plot in Woodyard Hammock over 6-year periods preceding (1978-84) and following (1986-92) Hurricane Kate.

Table 2.2. Numbers of recruits observed in the Woodyard Hammock plot before (1978-84), and after (1986-92) Hurricane Kate. Asterisks indicate significant differences between periods ($P < 0.05$).

	1978 -84	1986 - 92	
Overstory species:			
Magnolia grandiflora	5	10	
Fagus grandifolia	25	25	
Liquidambar styraciflua	6	71	*
Pinus glabra	0	416	*
Nyssa sylvatica	0	1	
Quercus michauxii	4	16	*
Quercus nigra	5	31	*
Carya glabra	11	14	
Liriodendron tulipifera	0	0	
Carya cordiformis	0	2	
Quercus virginiana	0	0	
Quercus alba	0	0	
Quercus shumardii	0	0	
Ulmus alata	2	1	
Pinus taeda	0	0	
Quercus hemisphaerica	2	3	
Magnolia virginiana	0	0	
Subtotal	60	590	
Understory species:			
Ilex opaca	35	31	
Carpinus caroliniana	42	223	*
Ostrya virginiana	65	899	*
Oxydendron arboreum	8	8	
Cornus florida	13	52	*
Acer rubrum	3	8	
Morus rubra	3	10	*
Symplocos tinctoria	81	76	
Prunus serotina	0	12	*
Osmanthus americanus	4	2	
Fraxinus pensylvannica	2	11	*
Cercis canadensis	1	1	
Cyrilla recemiflora	2	3	
Quercus stellata	0	0	
Sambucus canadensis	0	18	*
Rhus copollina	0	1	
Callicarpa americana	0	4	
Aralia spinosa	16	89	*
Ilex coriacea	0	1	
Cornus foemina	0	0	
Subtotal	275	1449	
Total	335	2039	

species with highest recruitment rates were the dominants *Ilex opaca*, *Carpinus caroliniana*, and *Ostrya virginiana* and the subdominant *Symplocos tinctoria* (Table 2.2). Among the overstory species, most recruits corresponded to either dominant or subdominant species (Table 2.2). However, recruitment rates varied among dominant and subdominant overstory species ranging from no recruitment, in *Pinus glabra*, *Nyssa sylvatica*, *Liriodendron tulipifera*, and *Carya cordiformis*, to 0.9 recruits.ha^{-1}.yr^{-1} in *Fagus grandifolia*. Rare overstory species had either low or no recruitment (Table 2.2).

In the post-hurricane period, mean rate of recruitment was 76.0 recruits.ha^{-1}.yr^{-1} - a 6-fold increase with respect to the pre-hurricane period. As before the hurricane, recruitment was more abundant for understory than overstory species (Figure 2.2). Among the understory species, the dominants *C. caroliniana* and *O. virginiana*, but not *Ilex opaca*, had very large increases in recruitment with respect to pre-hurricane levels (Table 2.2). Several subdominant and rare understory species also had significant increase in recruitment (Table 2.2).

Among the overstory species, two dominant (*Pinus glabra*, *Liquidambar styraciflua*) and two subdominant species (*Quercus michauxii*, *Q. nigra*) had significant increases in recruitment (Table 2.2). Most of the recruits of *P. glabra*, *Q. michauxii*, and *Q. nigra* were advance recruits 0.5 - 1.0 m tall at the time of the hurricane (W.J. Platt, personal observation). Field records indicate that at least 20% of the recruits of *L. styraciflua* in the post-hurricane period originated in root sprouts. The two overstory species with substantial recruitment rates before the hurricane (*Fagus grandifolia* and *Carya glabra*) maintained similar rates after the disturbance (Table 2.2). Recruitment rates of *M. grandiflora*, *N.*

sylvatica, *Liriodendron tulipifera*, and *C. cordiformis* remained low or null before and after the hurricane (Table 2.2). None of the rare overstory species, which had null or very low recruitment before, had increased recruitment after the hurricane (Table 2.2).

Tree growth

Species group comparisons.– Growth rate differences among combinations of species group by stratum, and between the pre- and post-hurricane periods, depended on tree dbh. The ANOVA model revealed significant differences among the parameters of the curves relating dbh with predicted growth in each class (Table 2.3). In the pre-hurricane period (1978-84), predicted growth of overstory pines increased significantly with tree size ($P < 0.05$) and, for trees > 30 cm dbh, was significantly higher than predicted growth of overstory hardwoods. In contrast, growth of overstory hardwoods was not significantly ($P > 0.05$) associated with tree dbh (Figure 2.3a). In the

Table 2.3. ANOVA table for the model comparing dbh increments between the pre-hurricane (1978-84) and the post-hurricane (1986-92) periods, among species groups (pines, overstory hardwood species, understory species) and strata (overstory and understory), initial dbh and dbh^2 as covariates nested within combinations of the three factors.

Source	Num. df.	Den. df.	F	*P*
Species group	2	4001	2.35	0.0959
Stratum	1	2713	1.50	0.2207
Species group x Stratum	2	2713	6.59	0.0014
Period	1	2713	245.99	0.0001
dbh (Group x Stratum x Period)	12	2713	19.74	0.0001
dbh^2 (Group x Stratum x Period)	12	2713	5.44	0.0001

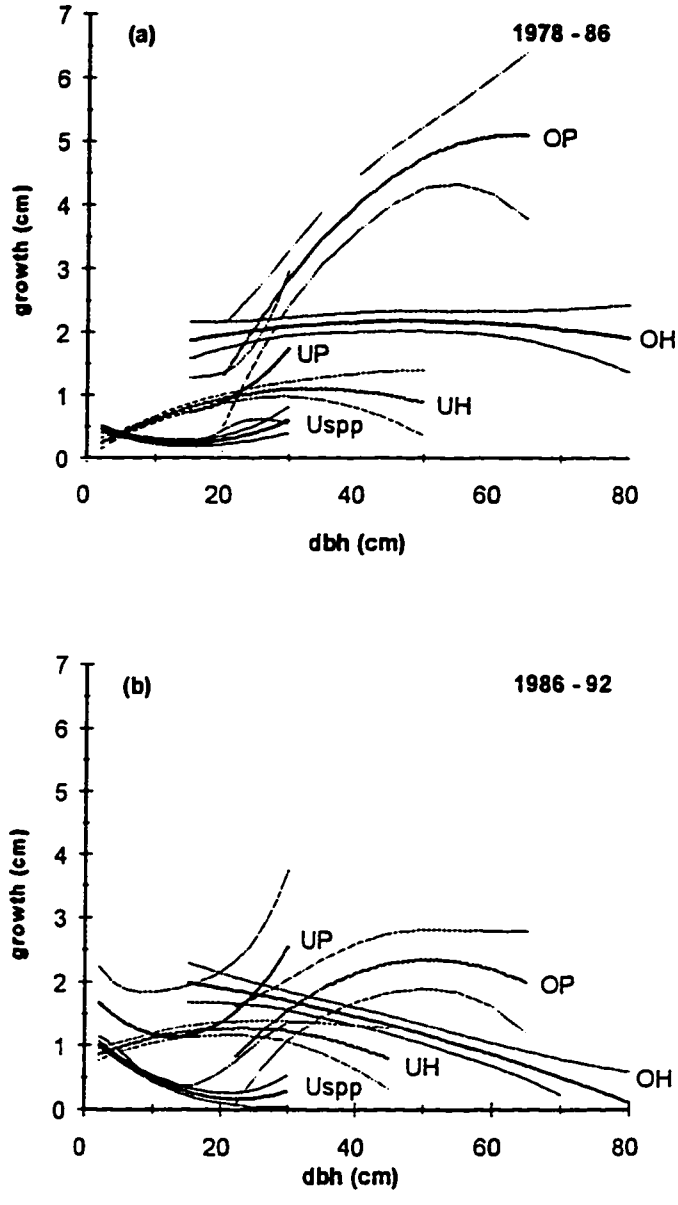

Figure 2.3. Association between expected diameter growth and diameter at 1.5 m height (dbh) in a 4.5 ha plot in Woodyard Hammock over 6-year periods preceding and following Hurricane Kate. (a) Pre-hurricane (1978-84), (b) Post-hurricane (1986-92). OH, overstory hardwoods; OP, overstory pines; UH, understory hardwoods; UP, understory pines; Uspp, understory trees of understory species.

understory stratum, predicted growth of small individuals (dbh < 30 cm) of hardwood overstory species increased with tree size. In contrast, for the understory species, predicted growth of individuals < 15 cm declined with tree size. Among understory trees > 5 cm dbh, but not smaller, growth was significantly higher for hardwood overstory species than for understory species. In addition, large understory hardwood trees had significantly lower growth than overstory trees of the same dbh (Figure 2.3a).

In the post-hurricane period (1986-92), predicted growth decreased for overstory trees, and increased for understory trees. In the overstory the post- than in the pre-hurricane period (Figure 2.3). In contrast, in the understory stratum, growth was significantly higher in the post- than in the pre-hurricane period for small trees of understory and overstory hardwood species (Figure 2.3). As a result, decline in growth of small individuals of understory species as dbh increased was more pronounced than before the hurricane; and increase in growth of understory trees of overstory species as dbh increased was less pronounced than before the hurricane (Figure 2.3). As in the pre-hurricane period, growth in the understory was significantly higher for hardwood overstory species than for understory species for trees > 5 cm dbh, but not for smaller trees. Large understory hardwood trees had significantly lower growth than overstory trees of the same dbh, but this difference was smaller than in the pre-hurricane period (Figure 2.3b).

Individual species comparisons.- Growth of saplings (trees 2 - 4 cm dbh) increased as a result of the hurricane. Mean sapling growth was significantly higher in the post- that in the pre-hurricane period ($P < 0.05$) for the dominant overstory *Fagus grandifolia*, for all three dominant understory species,

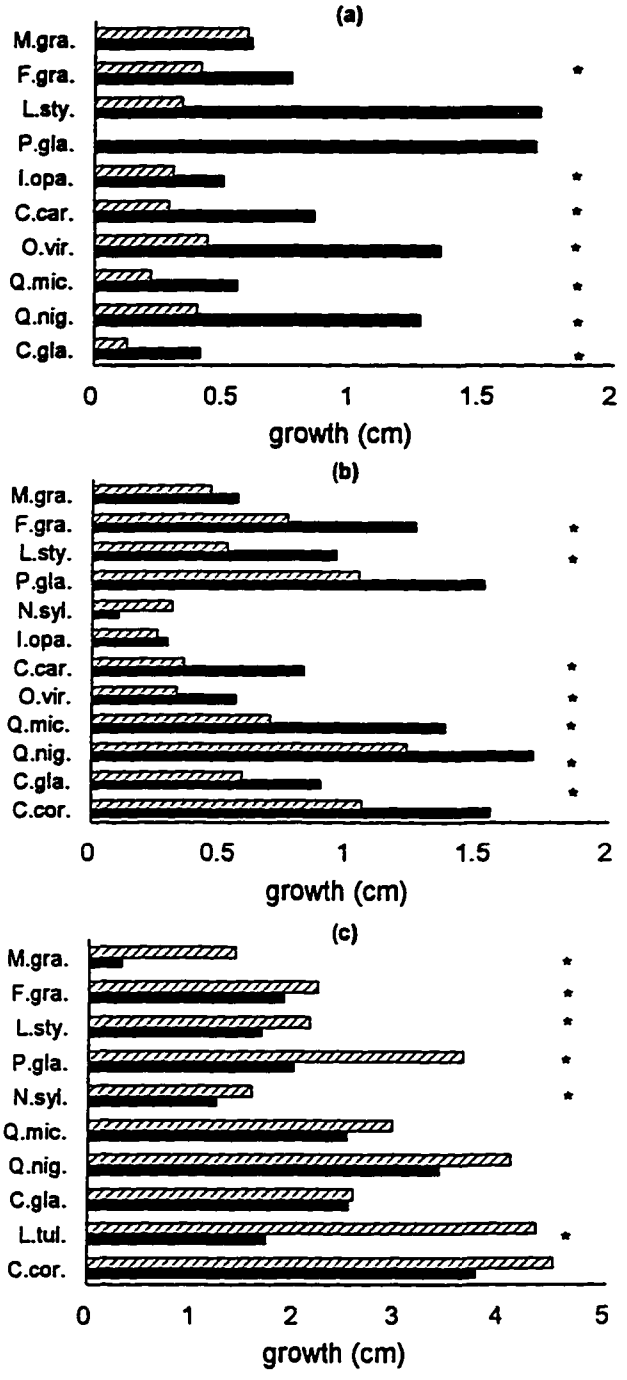

Figure 2.4. Mean diameter growth of dominant overstory and understory species and subdominant overstory species in Woodyard Hammock over 6-year periods preceding (1978-84, hatched bars) and following (1986-92, full bars) Hurricane Kate. (a) saplings (2cm ≤ dbh < 4 cm), (b) understory trees (dbh ≥ 4 cm), (c) overstory trees. Asteriscs indicate significant differences between periods ($P < 0.05$).

and of all subdominant overstory species with saplings in the plot (Figure 2.4a). In addition, newly recruited *Pinus glabra* saplings had high growth rate after the hurricane (Figure 2.4a). Among species with 30 or more saplings in the plot in 1978 (see Table 2.1), those with the highest mean sapling growth in the pre-hurricane period were *Fagus grandifolia*, *Ostrya virginiana*, and *Symplocos tinctoria*. In the post- hurricane period, in contrast, mean sapling growth was highest for *Pinus glabra*, and *O. virginiana*. (Figure 2.4a).

Growth of understory trees (dbh>4 cm) increased after the hurricane for most species. However, significant increases were less frequent among dominant overstory species than among dominant understory or subdominant overstory species. Two out of five dominant overstory species (*Fagus grandifolia*, *Liquidambar styraciflua*) had significantly higher mean growth of understory trees ($P < 0.05$) in the post- than in the pre-hurricane period. Mean growth did not change significantly between periods for understory *Magnolia grandiflora* ($P = 0.37$) and *Pinus glabra* ($P = 0.17$), and even decreased significantly ($P < 0.05$) for *Nyssa sylvatica* (Figure 2.4b). In contrast, mean growth of understory trees increased significantly ($P < 0.05$) for three out of four subdominant overstory species (*Quercus michauxii*, *Q. nigra*, *Carya cordiformis*); and for two (*Carpinus caroliniana*, *Ostrya virginiana*) out of three understory species (Figure 2.4b). As a consequence of these changes, the differences between faster growing and slower growing species increased after the hurricane, but the ranking changed only slightly. Mean dbh increment of understory trees was usually higher for overstory than for understory species. Among the overstory species, the highest mean growth rates in the understory corresponded to three subdominant (*Quercus nigra*, *Q. michauxii*, *Carya*

cordiformis) and two dominant (*Fagus grandifolia*, *Pinus glabra*) species (Figure 2.4b).

Growth of overstory trees decreased after the hurricane. However, this decrease was only significant ($P < 0.05$) for each of the dominant overstory species and for the subdominant *Liriodendron tulipifera* (Figure 2.4c). In contrast, mean growth of overstory trees of the subdominant *Quercus michauxii*, *Q. nigra*, and *Carya glabra* did not change significantly ($P > 0.15$). The largest reductions in mean growth after the hurricane corresponded to *L. tulipifera*, *Pinus glabra*, and *Magnolia grandiflora* (Figure 2.4c). Mean growth of dominant overstory species decreased significantly for both trees with and without major damage after Hurricane Kate ($P < 0.05$), except for trees of *Fagus grandifolia* without major damage ($P = 0.13$). Both before and after the hurricane, mean growth was typically higher for subdominant than dominant species; the main exception for this was the dominant *P. glabra* which had high growth in the pre-hurricane period (Figure 2.4e). Among dominant overstory hardwood species, *M. grandiflora* and *N. sylvatica* had the lowest mean growth rates (Figure 2.4e).

Mortality

Species group comparisons.– In the pre-hurricane period (1978-84), mortality of small trees decreased and mortality of large trees increased with tree size (Figure 2.5a). Association between mortality and tree dbh was significant within all combinations of species group by stratum (Table 2.4a). In the overstory stratum, for most dbh values, estimated mortality was significantly higher for pines than hardwoods (Figure 2.5a). In the understory, estimated mortalities declined with increasing tree dbh. This decline was more pronounced for pines and hardwood overstory species than for understory

Table 2.4. Wald tests for the logistic regression models relating tree mortality with stratum (understory or overstory), group (pine, hardwood overstory species, or understory species), and tree dbh (rounded to the nearest 0.5 cm). a) Pre-hurricane (1978-84) period; b) Direct mortality produced by Hurricane Kate; c) Post-hurricane (1986-92) mortality.

Source	d.f.	χ^2	*P*
(a) Pre - hurricane			
Intercept	1	6.97	0.01
Species group	2	17.03	< 0.01
dbh (hardwood overstory)	1	111.60	< 0.01
dbh^2 (hardwood overstory)	1	61.39	< 0.01
dbh (hardwood understory)	1	67.50	< 0.01
dbh (pine overstory)	1	18.56	< 0.01
dbh^2 (pine overstory)	1	11.20	< 0.01
dbh (pine understory)	1	10.75	< 0.01
dbh (understory species)	1	10.20	< 0.01
Goodness of fit (likelihood ratio)	393	348.87	0.95
(b) Hurricane			
Intercept	1	410.24	< 0.01
dbh (hardwood overstory)	1	12.49	< 0.01
dbh (hardwood understory)	1	3.63	0.06
dbh (pine overstory)	1	44.72	< 0.01
dbh^2 (pine overstory)	1	12.10	< 0.01
dbh (pine understory)	1	41.81	< 0.01
dbh (understory species)	1	19.84	< 0.01
Goodness of fit (likelihood ratio)	373	320.66	0.98
(c) Post-hurricane			
Intercept	1	33.40	< 0.01
Species group	2	14.41	< 0.01
dbh (hardwood overstory)	1	20.68	< 0.01
dbh^2 (hardwood overstory)	1	16.10	< 0.01
dbh (hardwood understory)	1	13.78	< 0.01
dbh (pine overstory)	1	0.53	0.47
dbh (pine understory)	1	2.85	0.09
dbh (understory species)	1	12.84	< 0.01
dbh^2 (understory species)	1	4.49	0.03
Goodness of fit (likelihood ratio)	348	355.55	0.38

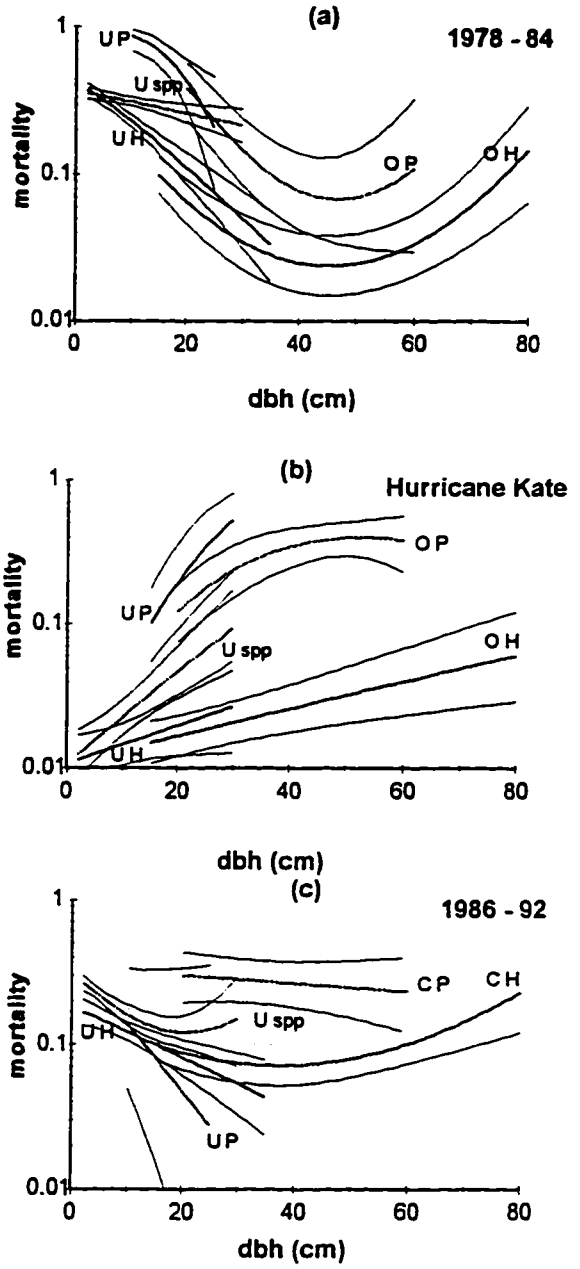

Figure 2.5. Logistic regression curves for the expected mortality of trees in a 4.5 ha plot in Woodyard Hammock, as functions of tree diameter at 1.5 m height (dbh). (a) Pre-hurricane mortality over the 6-year period 1978-84, (b) Direct hurricane mortality, (c) Post-hurricane mortality 1986-92 . OH, overstory hardwoods; OP, overstory pines; UH, understory hardwoods; UP, understory pines; Uspp, understory trees of understory species.

species (Figure 2.5a). For saplings (trees 2-4 cm dbh), estimated mortality was not significantly different between understory and overstory hardwood species. In contrast, for understory trees 4 - 20 cm dbh, mortality was significantly higher for pines than for hardwoods, and higher for understory than overstory hardwood species (Figure 2.5a).

Direct mortality produced by Hurricane Kate increased with tree size (Figure 2.5b). This increase was significant within most combinations of species group by stratum (Table 2.5b). Compared to the mortality over the preceding seven years, direct hurricane mortality was higher for overstory pines, similar for overstory hardwoods, and lower for understory species (Figure 2.5a,b). In the overstory, direct hurricane mortality was significantly higher for pines than hardwoods. In the understory, mortality of trees > 8 cm dbh was also significantly higher for pines than hardwoods, and was significantly higher for understory than for overstory hardwood species (Figure 2.5b). Direct hurricane mortality of saplings was very low (11 out of 767 trees).

In the post-hurricane period (1986-92), mortality variation with tree size was less pronounced than in the pre-hurricane period and than for direct hurricane mortality (Figure 2.5). However, estimated mortalities of overstory and understory hardwood species, but not of pines, were still significantly associated with tree dbh (Table 2.5c). Compared to pre-hurricane mortality, post-hurricane estimated mortality was higher for overstory trees and lower for understory trees (Figure 2.5a,c). In the overstory stratum, post-hurricane estimated mortality was significantly higher for pines than hardwoods. In the understory stratum, estimated pine mortality had large error; and estimated mortality in the understory was significantly lower for overstory than understory

hardwood species, although the differences were smaller that in the pre-hurricane period (Figure 2.5c).

Individual species comparisons.- Mortality of saplings (2 - 4 cm dbh), directly caused by Hurricane Kate was extremely low; and, after the hurricane, sapling mortality decreased with respect to pre-hurricane mortality for most dominant and subdominant species (Figure 2.6a). Estimated sapling mortalities in the post-hurricane period were significantly lower than in the pre-hurricane period ($P < 0.05$) for *Fagus grandifolia*, *Carpinus caroliniana*, and *Quercus michauxii* (Figure 2.6a). Sapling mortality differed significantly among dominant and subdominant species both before ($\chi^2 = 118.41$, 12d.f., $P < 0.01$), and after ($\chi^2 = 188.83$, 12d.f., $P < 0.01$) the hurricane. In both periods, *F. grandifolia* and *Ilex opaca* had the lowest estimated mortalities (Figure 2.6a).

Among understory trees (dbh>4 cm), Hurricane Kate caused substantial direct mortality of pines but low direct mortality of hardwood species, and resulted in decreased mortality of most tree species in the post-hurricane period. Significant mortality decreases were less frequent among dominant overstory species than among dominant understory or subdominant overstory species. Understory-tree mortalities were significantly lower in the post-hurricane than in the pre-hurricane period ($P < 0.05$) for: two out of five dominant overstory species (*Liquidambar styraciflua*, *Pinus glabra*), two out of three dominant understory species (*Carpinus caroliniana*, *Ostrya virginiana*), and three (*Quercus michauxii*, *Carya glabra*, *C. cordiformis*) out of four subdominant overstory species (Figure 2.6b). In the pre-hurricane period, understory-tree mortality differed significantly among species ($\chi^2 = 231.24$, 15 d.f., $P < 0.01$). Estimated mortality was lowest for *Fagus grandifolia* and *Ilex*

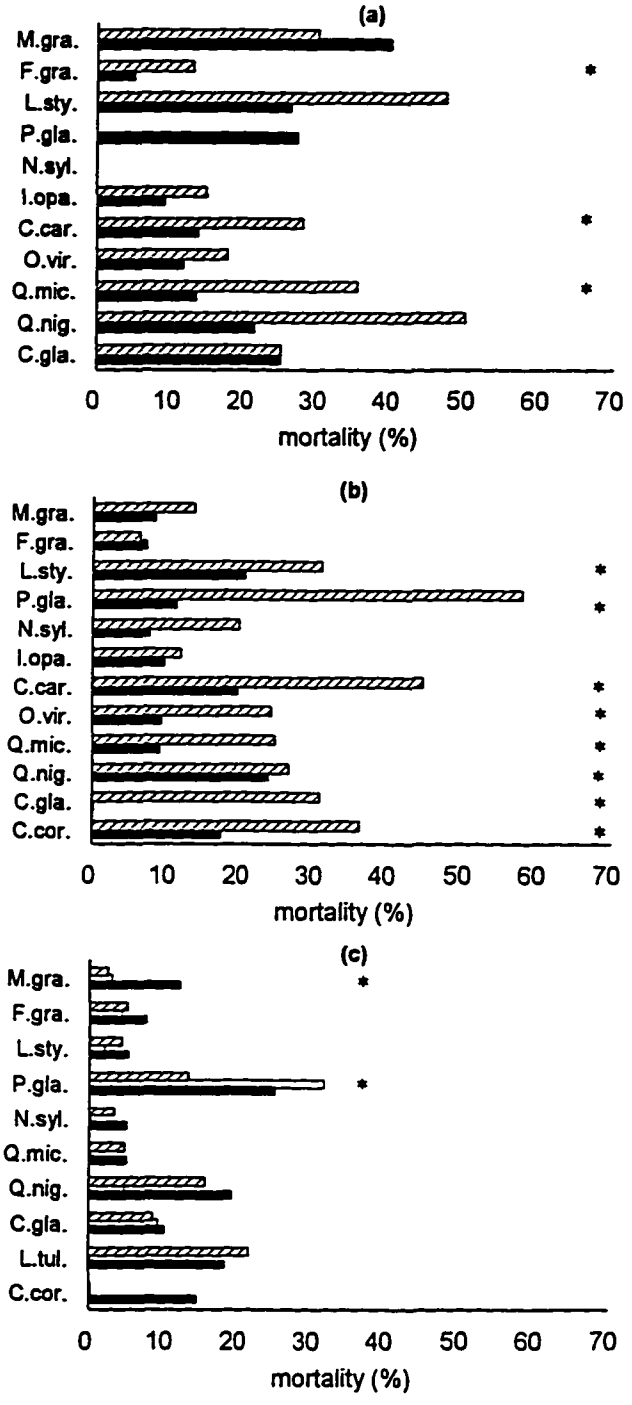

Figure 2.6. Mortality of dominant overstory and understory species and of subdominant overstory species in Woodyard Hammock. (a) saplings (2cm ≤ dbh < 4 cm), (b) understory trees (dbh ≥ 4 cm), (c) overstory trees. Hatched bars indicate mortality over the period 1978-84 preceding Hurricane Kate, full bars mortality over the period 1986-92 following Hurricane Kate, and empty bars overstory-tree mortality directly produced by Hurricane Kate. Asteriscs indicate significant differences between the pre- and post-hurricane periods ($P < 0.05$).

opaca and highest for *P. glabra* (Figure 2.6b). Direct hurricane mortality of understory trees was low (< 4%), and did not differ significantly (χ^2 = 6.4, 7d.f., P = 0.50), among dominant and subdominant hardwood overstory species. In contrast, direct hurricane mortality differed significantly among dominant understory species (χ^2 = 16.39, 2d.f., P < 0.01). *C. caroliniana* had 7.3 % mortality, while *I.opaca* and *O. virginiana* had less than 2.5 %. As in the pre-hurricane period, direct hurricane mortality of understory trees was highest for *P. glabra* (25 %; 0.95 confidence interval 12.6 % - 46.8 %). In the post-hurricane period, differences among species in understory tree mortality were smaller than before the hurricane (Figure 2.6b), but were still significant (χ^2 = 90.35, 14d.f., P < 0.01). Estimated mortalities were highest for *L. styraciflua*, *Quercus nigra*, and *C. caroliniana*, and lower for the remaining dominant or subdominant species (Figure 2.6b).

In the overstory, Hurricane Kate had little effect on the mortality of hardwoods but increased largely the mortality of pines, due to both direct and delayed effects. In the pre-hurricane period (1978-84), overstory tree mortality differed significantly among dominant and subdominant species (χ^2 = 24.57, 10d.f., P = 0.006). *Magnolia grandiflora* had the lowest and *Pinus glabra*, *Quercus nigra* and *Liriodendron tulipifera* the highest mortalities (Figure 2.6c). Direct hurricane mortality was significantly higher for overstory *P. glabra* than for dominant overstory hardwoods (χ^2 = 77.1, 1d.f., P < 0.005), but was not significantly different among hardwood overstory species (χ^2 = 3.3, 8d.f., P = 0.914). In the post-hurricane period (1986-92), mortality of overstory *Pinus glabra* and *Magnolia grandiflora* was significantly higher (P < 0.05) than in the pre-hurricane period, but mortalities of the other dominant and subdominant

species had not changed significant (Figure 2.6c). As in the pre-hurricane period, mortality of overstory trees differed significantly among dominant and subdominant species (χ^2 = 24.25, 9d.f., P = 0.004). *Pinus glabra* had the highest, while *F. grandifolia*, *Liquidambar styraciflua*, and *Nyssa sylvatica* the lowest mortalities (Figure 2.6c).

Growth/ mortality / basal area associations

Among dominant and subdominant species, mean growth of overstory trees tended to be lower for species with higher total basal area. Both before and after the hurricane, this was reflected in significant linear trends ($P < 0.05$) in overstory tree growth with log basal area (Figure 2.7a,b). For the understory trees (dbh ≥ 4 cm), these trends were muted and resulted in non-significant ($P > 0.05$) associations between basal area and mean dbh increments (Figure 2.7c,d).

Mortality of understory trees and saplings tended to be lower for species with higher total basal area both before and after the hurricane. For understory trees (dbh ≥ 4 cm), estimated pre-hurricane mortalities of dominant and subdominant species decreased significantly ($P < 0.05$) with increasing log total basal area (Figure 2.8a). After the hurricane, this trend was weaker but still significant (Figure 2.8b). Estimated sapling mortality among tree species with at least 20 saplings in the plot, decreased significantly with log total basal area ($P < 0.05$) both before and after the hurricane (Figure 2.8c,d).

Estimated mortality of overstory trees appeared not to be associated with total basal area. However, in the pre-hurricane period estimated mortality of overstory trees increased significantly with mean dbh increment ($P < 0.05$) for dominant and subdominant overstory species except *Carya cordiformis* (Figure

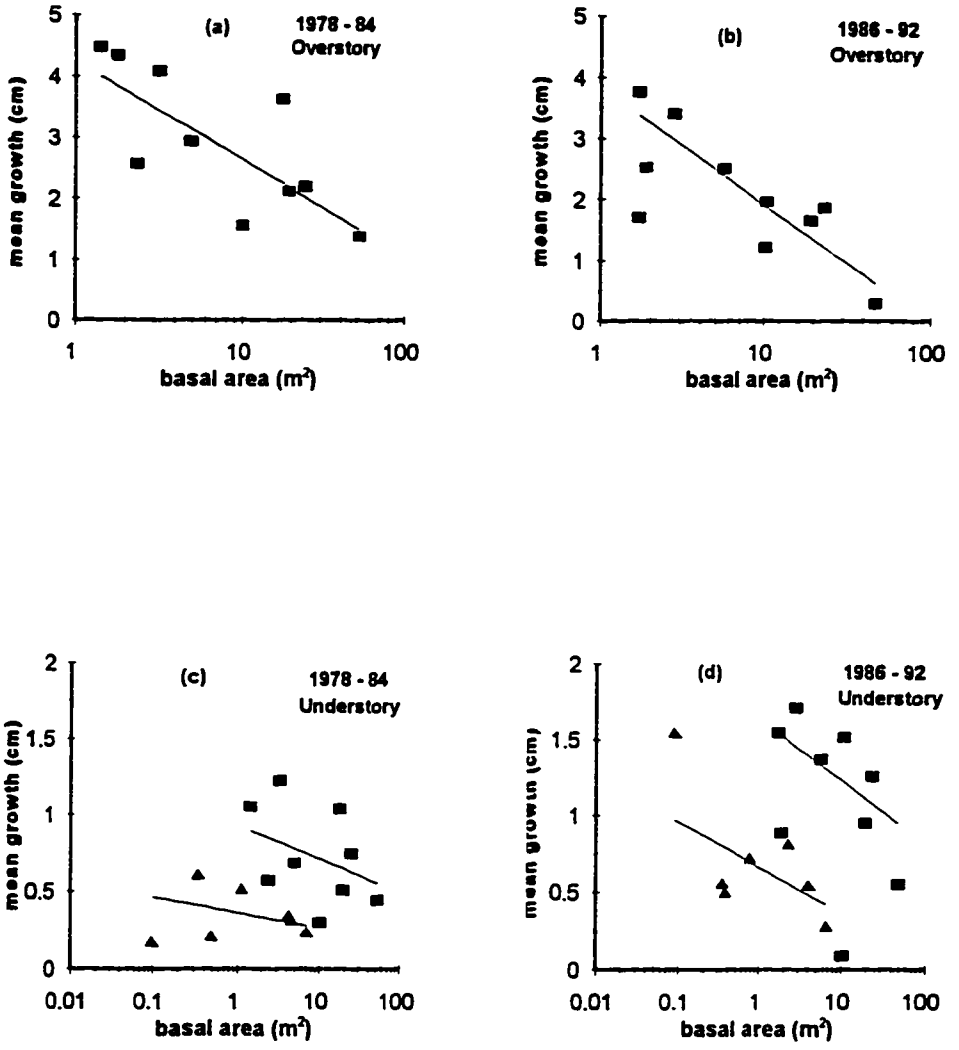

Figure 2.7. Association between species mean growth and log basal area in a 4.5 ha plot in Woodyard Hammock. (a) overstory trees in the pre-hurricane period, (b) overstory trees in the post-hurricane period, (c) understory trees (dbh ≥ 4 cm) in the pre-hurricane period (1978-84), (d) understory trees in the post-hurricane period (1986-92). Triangles correspond to understory and squares to overstory species. Each mean growth value was obtained from at least 20 trees.

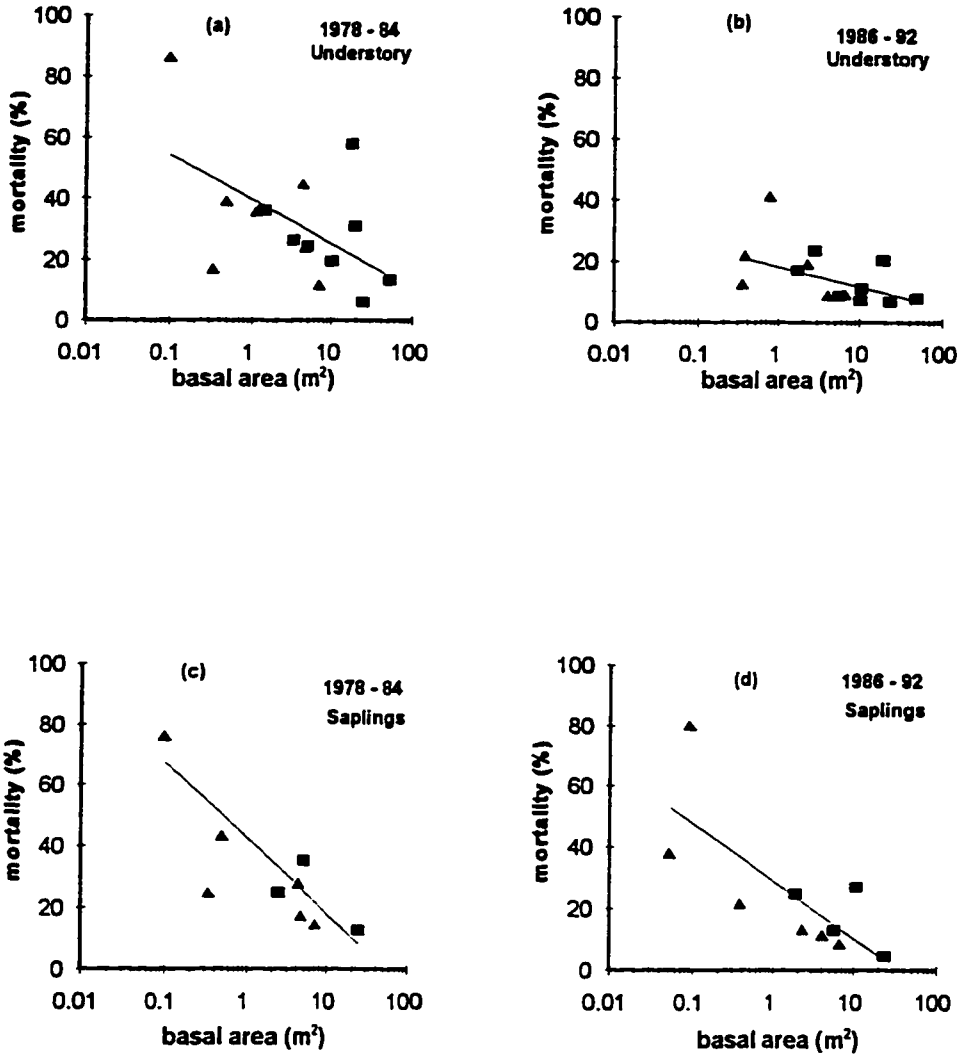

Figure 2.8. Association between species mortality and log basal area in a 4.5 ha plot in Woodyard Hammock. (a) understory trees (dbh ≥ 4 cm) in the pre-hurricane period, (b) understory trees in the post-hurricane period, (c) saplings (2cm ≤ dbh < 4 cm) in the pre-hurricane period (1978-84), (d) saplings in the post-hurricane period (1986-92). Triangles correspond to understory and squares to overstory species. Each estimate was obtained from at least 20 trees.

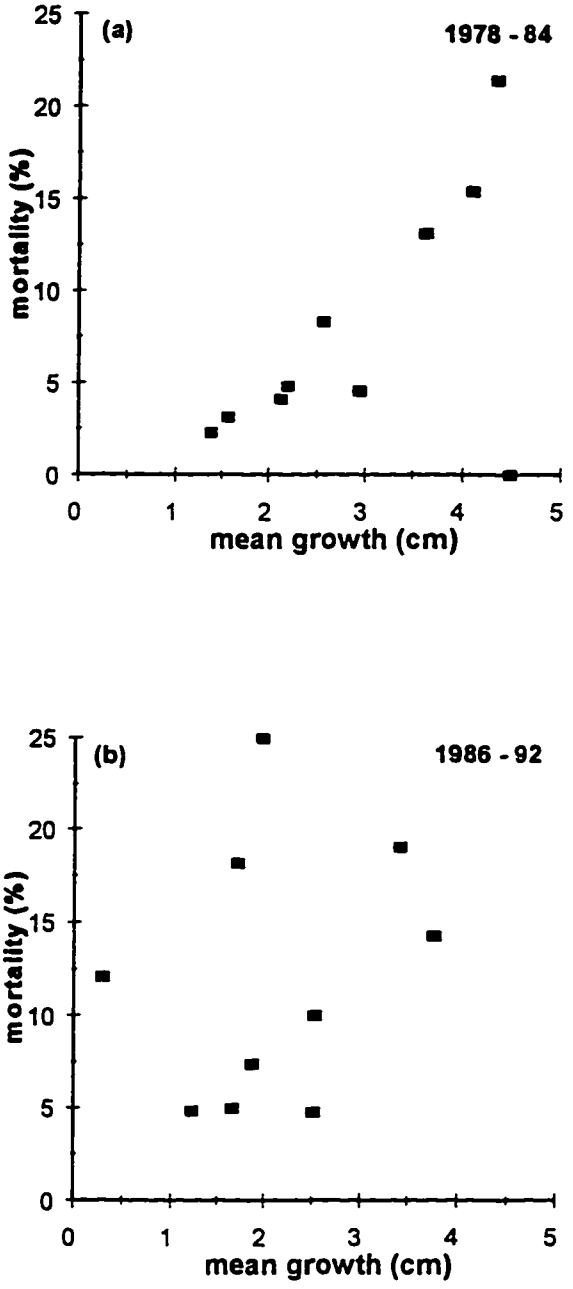

Figure 2.9. Association between mean growth and mortality of overstory trees of dominant and subdominant species in a 4.5 ha plot in Woodyard Hammock. (a) Pre-hurricane period (1978-84), (b) Post-hurricane period (1986-92).

2.9a). After the hurricane, mortalities of *Magnolia grandiflora*, *Liriodendron tulipifera* and *Pinus glabra* had increased disproportionately and this trend was not significant (Figure 2.9b).

DISCUSSION

Hurricane Kate separated two contrasting phases in the forest dynamics of Woodyard Hammock occurred between 1978 and 1992. In the pre-hurricane period, the rate of recruitment of trees into the smallest size classes was low, and recruitment was largely restricted to a few species. Rates of growth and survival were low for understory trees and high for overstory trees. Hurricane Kate produced extensive disruption of the canopy, damaging and killing mainly overstory trees. Within the overstory, the hurricane affected pines more than hardwoods (Platt et al. in review). This disturbance initiated a phase of increased recruitment, growth, and survival of understory trees, and decreased growth and survival of overstory trees (Batista and Platt 1996). However, patterns of species response to Hurricane Kate varied among tree species. As a consequence, hurricane disturbance appeared to have a different role in the setting of characteristic rhythms of regeneration, growth, and mortality of tree species with different life-history strategies.

Our analysis suggests that tree life-history strategies based on resistance to hurricanes, as opposed to those based on response after hurricanes, have been prevalent in Woodyard Hammock. While there appeared to be a trade-off between growth and survival of overstory trees, species with larger total basal area tended to have slower growth of overstory trees and higher survival of understory trees. In contrast, growth rates of understory individuals showed no significant association with basal area. Although

Table 2.5. Summary of demographic changes in Woodyard Hammock dominant and subdominant tree species after Hurricane Kate in 1985. Rate changes in this table are based in comparisons between the periods 1978-84 (pre-hurricane) and 1986-92 (post-hurricane). Entries "Increased", or "Decreased", in the table indicate significant differences ($P < 0.05$) between these two periods. The symbol * indicates that direct hurricane mortality of the corresponding species was comparatively high. Based on the observed demographic patterns, a "strategy" was attributed to to each species according to whether hurricane resistance or response after hurricane disturbance appeared to be most critical for population persistence.

	Understory			Overstory stratum		"Strategy"
	Recruitment	Growth	Survival	Growth	Survival	
Overstory species						
Dominant:						
Magnolia grandiflora				Decreased	Decreased	Resistance
Fagus grandifolia		Increased		Decreased		Resistance
Liquidambar styraciflua	Increased	Increased	Increased	Decreased		Resistance/Response
Pinus glabra	Increased		Increased*	Decreased	Decreased*	Response
Nyssa sylvatica		Decreased		Decreased		Resistance
Subdominant:						
Quercus michauxii	Increased	Increased	Increased			Resistance/Response
Quercus nigra	Increased	Increased				Resistance/Response
Carya glabra		Increased	Increased			Resistance?
Carya cordiformis			Increased			Resistance?
Understory species						
Dominant:						
Ilex opaca						Resistance
Ostrya virginiana	Increased	Increased	Increased			Response
Carpinus caroliniana	Increased	Increased	Increased*			Response

response to hurricane disturbance, such as increased recruitment, growth, or survival of released understory trees, occurred to some extent for most dominant and subdominant species, resistance appeared to be critical for most of them (Table 2.5). Tree survival to the hurricane was very high for most dominant and subdominant species; and appeared to be critical for the persistence of the dominant overstory hardwoods *Magnolia grandiflora*, *Fagus grandifolia*, and *Nyssa sylvatica*, and of the dominant understory *Ilex opaca* (Table 2.5). Persistence of *Liquidambar styraciflua* and the subdominant overstory species appeared related to a combination of resistance and response to hurricane disturbance. These resistant dominant species accounted for about 80 % of the total basal area throughout the period 1978-1992. In contrast, persistence of three dominant species, the overstory *Pinus glabra*, and the understory *Ostrya virginiana* and *Carpinus caroliniana*, appeared to depend critically on their capacity to respond after the disturbance (Table 2.5). Throughout the period 1978-1992, these three species accounted for 12 to 18 % of the total basal area. Within these groups of species apparently dependent on resistance or on response, the different species showed individualistic demographic behavior in relation to the hurricane.

Life histories of individual species

Magnolia grandiflora, the main dominant species in Woodyard Hammock, showed no response to the canopy openings but substantial resistance to the disturbance produced by Hurricane Kate. After the disturbance, there were no significant changes in recruitment, growth, or survival of understory *M. grandiflora* (Table 2.5). In fact, recruitment of this species has been infrequent for many decades in Woodyard Hammock. Based on the size frequency

distribution and age-size relations, Blaisdell et al. (1974) inferred that trees less than 65 years old were under-represented in this population. In the period we studied, the size frequency distribution of this population (not shown) also had a gap in the smaller size classes. Platt and Hermann (1986) and Platt and Schwartz (1990) hypothesized that large-scale disturbance would be necessary for recruitment of *M. grandiflora* in Woodyard Hammock. These authors, as well as Blaisdell et al. (1974) expected clonal growth to have an important role in the dynamics of *M. grandiflora* populations. However, both before and after Hurricane Kate, this species exhibited little sprouting from tree bases or from roots. On another hand, mortality of *M. grandiflora* directly produced by Hurricane Kate was low. Life span of these trees can be very long, as oldest individuals in Woodyard Hammock are well above 200 years old, and they are likely to undergo many hurricanes (Blaisdell et al. 1974, Batista and Platt 1996). Despite significant decreases in overstory tree growth and survival after the hurricane, *M. grandiflora* remained the main dominant overstory species in the forest. Over the period we examined, and possibly over at least most of the last century, resistance to hurricane disturbance and survival of overstory trees have been the key for the persistence of *M. grandiflora* as an overstory dominant in Woodyard Hammock.

While persistence of *Magnolia grandiflora* in Woodyard Hammock appears to depend on hurricane resistance and survival, our data do not reveal the conditions necessary for this species to regenerate at substantial rates. One explanation for the paucity of regeneration might be based on perturbations of background environmental conditions. In Woodyard Hammock, frequency of creeping fires entering the forest is likely to have decreased after replacement

of the pine savannas on the nearby uplands (Blaisdell et al. 1974, Batista and Platt 1996). Also, patterns of drainage could have changed as a consequence of the alteration of the surrounding vegetation, of possible changes of the level of Lake Iamonia, or of the construction of a dirt road nearby (Blaisdell et al. 1974). Another possible explanation for low regeneration rate is related to what we will name here the self-inhibition hypothesis. While paucity of *M. grandiflora* recruitment has been noticed in forests in which this species is abundant in the overstory (Kurz 1944, Quarterman and Keever 1962, Blaisdell et al. 1974), substantial recruitment has been found in forests in which the canopy is dominated by pines or deciduous hardwoods (Blaisdell et al. 1974, Harcombe and Marks 1983, Glitzenstein et al. 1986). Peters and Platt (1996) proposed that, because *M. grandiflora* is evergreen, understory individuals under a predominantly deciduous canopy could benefit from increased light intensity in warm winter days; the lack of such seasonal release under a predominantly evergreen canopy might restrict their survival and eventual recruitment into the canopy. If a mechanism of self-inhibition was acting, recruitment and survival of this species in the understory would be frequency-dependent (cf. Connell et al. 1984). In this case, this population would have non-equilibrium dynamics; regeneration would become substantial only if the density of overstory individuals were reduced by aging and accumulation of damage by multiple hurricanes.

Fagus grandifolia exhibited limited response but substantial resistance to Hurricane Kate. Responses of understory *Fagus grandifolia* were restricted to significant increases of sapling growth and survival, and of understory tree growth. For this species, both recruitment and survival of understory trees were

high in the pre-hurricane period, and remained similar after Hurricane Kate. Resistance to disturbance, in contrast, was reflected in low direct hurricane mortality and in absence of significant change of overstory-tree mortality after the hurricane (Table 2.5). In addition, overstory trees without major hurricane damage had no significant decrease in mean growth rate. A detailed demographic study showed that this population was very close to equilibrium; and that the vital rates most influential for its persistence were the survival rates of large understory and small overstory trees (Batista et al. in review). In addition, that study showed that the increases in sapling growth and survival and in understory tree growth brought about by the hurricane had little effect on the long-term population trend. This description suggests that resistance to hurricane disturbance, rather than the ability to respond after the disturbance, is critical for persistence and abundance of *F. grandifolia* in Woodyard Hammock.

Two species, the understory dominant *Ilex opaca* and the overstory subdominant *Carya glabra*, exhibited demographic patterns somewhat similar to those of *F. grandifolia*. Both species had substantial recruitment before Hurricane Kate, and no significant change in recruitment, sapling growth, or in overstory tree growth and mortality after the hurricane (Table 2.5). *Carya glabra*, had somewhat higher direct hurricane mortality of overstory trees, and significant increase in understory tree survival. In contrast, *I. opaca*, had low direct hurricane mortality and no change in understory tree survival. As an understory species, *I. opaca* has been hypothesized to behave as a fugitive (Peters and Platt 1996); however, this species would depend little on gaps (cf. Harcombe and Marks 1983). Because *I. opaca* is evergreen, trees of this species might extend their growing season taking advantage of periods of

reduced canopy density. These data suggest that resistance and consequent survival are more likely to be critical than responses to large scale disturbance for the persistence of *I. opaca* and *C. glabra* in Woodyard Hammock.

The life-history strategy of *Liquidambar styraciflua* appears to combine response and resistance to hurricane disturbance. This dominant hardwood overstory species showed a pulse of recruitment after Hurricane Kate (Table 2.5), in part as a result root sprouting (cf. Kormanik and Brown 1967). Saplings and understory individuals of this species are shade-intolerant (Baker 1949, Blaisdell et al. 1974, Kormanik 1990), and under the closed-canopy pre-hurricane conditions had relatively low growth and substantial mortality. In contrast, the overstory trees, which usually emerge above the canopy (Peters and Platt 1996), had high survival and substantial growth. As noted by Fowells (1967), trees of *L.styraciflua* have been noted to be very resistant to wind damage; in Woodyard Hammock overstory *L. styraciflua* had little direct hurricane mortality and no significant change in survival during the post-hurricane period (Table 2.5). After Hurricane Kate, growth sof aplings was high; and growth and survival of understory trees increased significantly (Table 2.5). Rapid growth of clonal recruits appears to be supported by root reserves (Kormanik 1990). As growth pattern in this species favors height growth, these understory individuals would have relatively high chance of reaching the canopy (Peters and Platt 1996). Ramets that reach the overstory in Woodyard Hammock can live more than 200 years (Batista and Platt 1996) and, therefore, undergo several hurricanes during their lives. In Woodyard Hammock, the population of *L. styraciflua* would consist of several coexisting cohorts of ramets, each presumably originated after an episode of extensive canopy

disruption. Indeed, tree core data obtained before Hurricane Kate indicated a discontinuous age distribution in this population, with the last recruitment pulse shortly after the 1941 hurricane (Platt 1984). According to these results, combined wind resistance and rapid response to increases in light levels produced by hurricanes would account for the abundance of *L. styraciflua* in Woodyard Hammock. We suggest that, because most adult individuals in this population would be able to survive hurricanes, the demography of this species would be relatively insensitive to variations in hurricane frequency.

Quercus michauxii, and *Q. nigra*, the two most abundant oak species in Woodyard Hammock, responded to Hurricane Kate with significant increases in recruitment and growth of saplings and understory trees. In addition, saplings and understory trees of *Q. michauxii* had significantly increased survival (Table 2.5). However, the significance of this response for the persistence and abundance of these species in Woodyard Hammock is not clear. Analyses performed before the hurricane suggested that these species would be recruited into the understory in localized gaps in the absence of large-scale disturbances (Platt and Hermann 1986). However, actual recruitment into the understory in the pre-hurricane period was rather low. Therefore, if recruitment were limiting, growth in localized gaps might not be sufficient to account for the local persistence of these species; while release of many suppressed individuals in the post-hurricane period could be critical for the persistence of these species. On another hand, overstory individuals of these species had low direct hurricane mortality and no significant decrease in growth or survival after the hurricane (Table 2.5). Resistance of these overstory trees could also be critical for population persistence. Although it is unclear which characteristic is

most important, both response after hurricane by released understory individuals and hurricane resistance of overstory trees are present in life history of these oak species in Woodyard Hammock.

Pinus glabra was the tree species whose persistence and abundance in Woodyard Hammock appeared most closely linked to response after hurricane disturbance. This species consistently had high mortality: in the pre-hurricane period, as a direct effect of Hurricane Kate, and in the post-hurricane period. In addition, *P. glabra* had no recruitment in the pre-hurricane period but had a recruitment pulse *P. glabra* after the hurricane (Table 2.5). This essentially resulted in the replacement of one cohort by another. Recruitment of this species after Hurricane Kate resulted mostly from the release of advance recruits that were present in localized gaps at the time of the storm (Platt and Schwartz 1990, Platt and Hermann 1986). After these gaps were augmented, these recruits grew rapidly, probably in relation with a relatively high allocation to foliage (Strauss and Ledig 1985). In addition, as they grow preferentially in height, some of these trees are likely to rapidly attain canopy stature (Peters and Platt 1996). Seed production may begin after 10 years, and be maximum after 20 to 40 years (Sargent 1941). While reported potential longevity of *P. glabra* is 112 years (Strauss and Ledig 1985), in Woodyard Hammock, the oldest adults of this species were less than 50 years old (Batista and Platt 1996). Apparently, cohort replacement after hurricane disturbance has been recurrent in this species. Data from tree cores obtained before Hurricane Kate revealed that, at that time, most of the population of *P. glabra* consisted of trees recruited after the 1941 hurricane (Hirsh and Platt 1981). Life history of *P. glabra* appears to be largely tied to the intervals between hurricanes. Each

hurricane would decimate the adult population and initiate a new cohort based on the extant bank of advance recruits. The number and spatial distribution of gaps containing these advance recruits at the time of the hurricane would be the main determinant of density and spatial distribution of the new cohort. Trees of this new cohort would rapidly reach the canopy, and begin producing advance recruits in localized gaps. As trees of *P. glabra* have high mortality, their density would decline rapidly during the interval between hurricanes. For this reason, extended intervals between hurricanes could compromise the persistence of *P. glabra* in this forest.

Demographic patterns of *Ostrya virginiana* and *Carpinus caroliniana*, two of the three dominant understory species in Woodyard Hammock, were strongly affected by Hurricane Kate. While recruitment of these species occurred before the hurricane, rates of recruitment increased massively after the disturbance. Likewise, mean growth and survival of established trees increased in response to Hurricane Kate (Table 2.5). These changes resulted in the expansion of these populations during the post-hurricane period. However, this expansion is likely to be followed by a decline unless large-scale canopy disturbance recurred with unusual frequency.Growth and survival did not tend to increase with tree size for *O. virginiana*, and tended to decrease for *C. caroliniana*. As a consequence, in the absence of disturbance, individuals of these understory species are likely to be outgrown by longer-lived trees of overstory species. Regeneration and release after the hurricane resulted in rapid increases in the densities of these populations and would likely be essential for long-term maintenance of their dominance in the understory. However, long-term persistence of these populations might not critically depend on large-scale

disturbance. In the pre-hurricane period, recruitment and growth of these two species was substantial in localized canopy gaps (Platt and Schwartz 1990). Also, large individuals of these species often occupy patches with no overstory species where they could be eventually replaced by a new tree of an understory species (Peters and Platt 1996). In any event, rapid regeneration and growth in gaps, rather than ability for long-term survival, appears to be the key strategy for these two understory species.

Resistance and response to hurricanes at the forest level

The bulk of recent studies on hurricane damage and early stages of forest recovery suggest that the combination of extensive damage and limited mortality is the most common outcome of hurricane disturbance (e.g. Lugo et al. 1983, Foster 1988, Boucher et al. 1990, Brokaw and Grear 1991, Brokaw and Walker 1991, Frangi and Lugo 1991, Gresham et al. 1991, Armentano et al. 1995, Foster and Boose 1992, Baldwin et al. 1995, Noel et al. 1995, Slater et al. 1995, Platt et al. in revision). This is an indication that resistance to disturbance may be prevalent in many hurricane-frequented forests. In areas like the coastal plain of the northern Gulf of Mexico, where hurricanes are frequent enough to recur within the life span of individual trees, these disturbances would exert selection pressures tending to increase the average fitness of tree populations (i.e. they are disasters rather than catastrophes, Harper 1977). Under such a selection pressure, adaptations for resistance would typically be advantageous over adaptations for rapid response canopy disruption. We suggest that the probability of resistance appearance would decrease with the intensity of the disturbances, and increase with time of exposure to the disturbance regime. In fact, hurricanes that affect the coastal plain of the northern Gulf of Mexico

usually reach the coastline with lower intensity than those entering the Florida peninsula, and quickly lose strength as they travel inland (Neumann et al. 1992). Coincidently, although other environmental stresses are likely to interact with disturbances, mangrove forests of southern Florida, which are affected by a regime of more intense storms than Woodyard Hammock, are dominated by tree species that have high mortality and rapid regeneration (Baldwin et al. 1995). The time that the tree species present in Woodyard Hammock have been exposed to a regime of frequent hurricanes is not known. However, palynological data suggest that the climate along the northern Gulf of Mexico has been relatively stable at least during the Holocene (Prentice et al. 1991) and possibly through the Pleistocene (Delcourt and Delcourt 1987, Webb 1990). In addition, the fact that the dominant *Pinus glabra*, an endemic to Southern Mixed Hardwood Forests (Kossuth and Michael 1990), appeared to be highly dependent on frequent large-scale disturbances, suggests that hurricanes have been a rather consistent element of the environment of the region.

The relative role of resistance and response to disturbance is related to hypotheses of tree species coexistence and forest dynamics. A necessary condition for continued coexistence of tree species is that the different populations do not jeopardize the most critical vital rates of each other. According to different conceptual models, such a condition could occur as a result of: chance (Hubbell 1979), distance (mass effects, Shmida and Wilson 1985), environmental fluctuations (Chesson and Warner 1981), disturbance (Loucks 1970, Connell 1978, Huston 1979, White 1979), and niche partitioning (Grubb 1977, Ricklefs 1977, Denslow 1980, 1985, Tilman 1988, Connell et al.

1984, Poulson and Platt 1996, etc.). Models based on niche partitioning have usually stressed the role of regeneration (Janzen 1970, Connell 1971, Grubb 1977, Harper 1977, Ricklefs 1977, Denslow 1980). However, while regeneration is necessary for the indefinite persistence of any population, other processes along the life cycle could become more limiting and buffer differences in regeneration. In fact, there is growing evidence that survival of individuals of high reproductive value, and not actual reproduction, is often the most critical vital rate in tree populations (Gotelli 1991, Silvertown and Franco 1993, Silvertown et al. 1993, Batista et al. in review). In contrast, the importance of regeneration niche specialization has been demonstrated in only "a few light-demanding species" of trees (Denslow et al. 1990, Denslow 1995). Typically, regeneration would likely be the limiting process for short-lived, light-demanding species that respond after a disturbance by rapidly capturing released resources, while survival would likely be the limiting process for long-lived, shade-tolerants specialized for resistance to disturbance.

In Woodyard Hammock, multiple mechanisms of species coexistence appear to contribute to maintaining species diversity. This forest was composed of a relatively stable matrix dominated by long-lived overstory hardwoods, dotted with more dynamic patches dominated by short-lived *Pinus glabra* or deciduous understory species (Peters and Platt 1996). Within the dynamic patches, dominant populations would be limited by regeneration opportunities; and species coexistence could result from regeneration niche partitioning if pines and understory species became established in patches with different histories of disturbance. Indeed, juveniles and saplings of *P. glabra* and understory species appear to be spatially segregated within gaps (W.J. Platt

and W.B. Batista personal observation). Within the hardwood matrix, dominant populations would be limited by tree survival. Survival of individuals with high reproductive value, critical for these populations, could be accounted for by differences among growth patterns of various species (Harcombe and Marks 1977, Peters and Platt 1996, Poulson and Platt 1996), or it could, in some cases, result from frequent release by hurricane disturbance. While the trends observed in demographic rates of species with increasing dominance suggest that most of these populations might tend towards equilibrium, compensatory mechanisms resulting in non-equilibrium dynamics could be preventing *Magnolia grandiflora* from overtaking the forest (cf. Connell et al. 1984). These hypotheses of species coexistence within the two structural elements, the overstory-hardwood matrix and the pine-understory species patches, call for specific research. It is the coexistence between these two structural elements what, according to our results, appears to be main effect of hurricane disturbance in Woodyard Hammock. Hurricanes that affect Southern Mixed Hardwood Forests would be frequent enough to provide the limiting regeneration conditions for those species specialized in response to canopy opening, and mild enough not to compromise the critical survival of those dependent on resistance.

Chapter 3

Demography of a Shade-tolerant Tree (*Fagus grandifolia*) in a Hurricane-disturbed Forest

INTRODUCTION

The combination of shade-tolerance, limited response to high levels of light, and long life-span is typically associated with trees in closed-canopy forests (Marks 1975, Bazzaz 1979, Swaine and Whitmore 1988). One of the most exemplary shade-tolerant species is *Fagus grandifolia* Ehrh. (American beech), a deciduous tree common in temperate forests of eastern North America (Braun 1950). The autoecology of this species has been studied extensively. Light is not required for germination of seeds (Rudolf and Leach 1974) or sprouting of root buds of *F. grandifolia* (Jones and Raynal 1988). Seedlings and saplings survive and grow in shade (Harcombe et al. 1982, Platt and Hermann 1986, Canham 1988, Jones and Raynal 1987, Tubbs and Houston 1990, Poulson and Platt 1995), probably due to their low respiration rate and high photosynthetic efficiency at low light (Loach 1967, Wood and Turner 1971), as well as their pattern of ramification that minimizes self-shading and investment in supporting structures (Canham 1988, Küppers 1989). Small *F. grandifolia* have higher growth rates in small gaps than under canopy trees (Canham 1988, 1990, Poage and Peart 1993, Poulson and Platt 1995). However, growth rates in gaps are not correlated with light level, possibly due to low light-saturation intensity (Loach 1967), limited seasonal extension growth (Moore 1909) and relatively low morphological plasticity (Canham 1988, 1989, Poulson and Platt 1995). Individuals of *F. grandifolia* can live longer than many

species with which they co-occur (Altman and Dittmer 1962, Tubbs and Houston 1990, Poulson and Platt 1995). In addition, community-level analyses of temperate forests have suggested that *F. grandifolia* usually reaches the canopy in small gaps. Relative abundance of this species has been proposed to increase during periods of low rate of canopy disturbance and decline when the rate of canopy disturbance is high (Mac Gowan 1937, Blaisdell et al. 1974, Forcier 1975, Barden 1980, Harcombe et al. 1982, Runkle 1982, Glitzenstein et al. 1986, Canham 1988, 1990, Poulson and Platt 1989, 1995, Platt and Schwartz 1990, Brisson et al. 1994, Peters and Platt 1995).

Notwithstanding its proposed association with low rates of canopy disturbance, *Fagus grandifolia* often is a major component in hurricane frequented hardwood forests along the Atlantic and Gulf coasts from New England to eastern Texas (Foster 1988, Platt and Schwartz 1990, Merrens and Peart 1992, Bill and Harcombe 1994, Batista and Platt 1996). In particular, Southern Mixed Hardwood Forests located along the Coastal Plain of the northern Gulf of Mexico, from northern Florida to eastern Texas, consistently have *F. grandifolia* among the dominant species (Quarterman and Keever 1962). Each stand of these forests is likely to be affected several times per century by moderately intense tropical storms (maximum sustained windspeeds 100 - 160 km/hr, Batista and Platt 1996). These storms damage overstory trees, create multiple tree-fall gaps, expand the fraction of the forest area in gaps, and increase the light levels under the canopy. Following the storms, damaged overstory trees exhibit decreased growth rates, while understory trees not damaged by fallen trees are released (Batista and Platt 1996). In these forests, *F. grandifolia* coexists with both evergreen (*Magnolia grandiflora*, *Pinus* spp.)

and deciduous (*Liquidambar styraciflua*, *Quercus* spp., *Carya* spp., *Nyssa sylvatica*) overstory species, and with many understory species (e.g. *Ostrya virginiana*, *Carpinus caroliniana*, and *Ilex opaca*) (Gano 1917, Quarterman and Keever 1962, Delcourt and Delcourt 1974, Blaisdell et al. 1974, Marks and Harcombe 1981, Glitzenstein et al. 1986, White 1987, Ware et al. 1993, Platt and Schwartz 1990, Vankat 1990, Batista and Platt 1996).

How does *Fagus grandifolia* persist under a regime of frequent canopy disruption? We addressed this primarily demographic problem by examining the responses of a population of *F. grandifolia* to a moderate-intensity hurricane in a Southern Mixed Hardwood Forest. For our analysis, we distinguished two phases in the dynamics of the forest: the "open" canopy, and the "closed" canopy periods. The "open" canopy phase was defined as that starting with a hurricane, over which some large fraction of the forest area was in multiple tree-fall gaps. Immediate and delayed tree deaths caused by the hurricane were included in the mortality of this period. The "closed" canopy phase was defined as that occurring some time after the most recent hurricane, when the canopy had reformed and a comparatively large proportion of the forest was under canopy or in small, single-treefall gaps. These two phases were assumed to alternate in time in some long-term stochastic sequence. Admittedly, our analysis is dependent on this particular definition of phases of forest dynamics, but this type of dependance is intrinsic to the perception of many ecological systems (O'Neill et al. 1986, Orloci and Orloci 1988).

We formulated four alternative hypotheses that might explain the apparent persistence of local populations of *Fagus grandifolia* under the natural sequence of "closed" and "open" canopy periods (see Table 3.1). In hypothesis

one (resistance), we proposed that hurricane related damage and mortality may be not severe enough to affect the projected stability of population size. The size of the population would tend to remain stable in both "closed" and "open" canopy periods. In hypothesis two (recovery), we proposed that the population may persist because intervals between hurricanes would be long enough to allow the population to recover during the "closed" canopy period. The size of the population would tend to decline in the "open" canopy period, but this trend would be balanced by an increasing trend after the canopy has been restored. In hypotheses three and four, we postulated that persistence of *F. grandifolia* may be dependent upon recurrent disturbance (cf. Peters and Poulson 1994). In hypothesis three (release), we proposed that the size of the population would tend to increase over the "open" canopy phase when understory trees and seedlings receive increased light. This trend would balance, over the long term, a negative trend that would occur in the "closed" canopy phase. In hypothesis four (complementation), we proposed that the population would only persist if

TABLE 3.1. Population trends predicted by four hypotheses proposed to explain the long term persistence of *Fagus grandifolia*. The "open" canopy phase starts with a hurricane and includes the time when a large fraction of the forest is in multiple tree-fall gaps. The "closed" canopy phase occurs after the canopy has been restored from the most recent hurricane damage and a comparatively large fraction of the forest is under canopy or in single-treefall gaps.

Hypothesis	"Open"	"Closed"	Long-term
resistance	Stable	Stable	Stable
recovery	Negative	Positive	Stable
release	Positive	Negative	Stable
complementation	Negative	Negative	Stable

"closed" and "open" canopy periods alternated in time. This would happen if some critical life-history process occurred at a sufficient rate only during one of the phases, while other such process only occurred at sufficient rates during the other phase (e.g. sufficient growth to maturity might occur only in "open" and sufficient recruitment only in "closed" canopy phases). The long-term trend of population size would be declining if either the "closed" or the "open" canopy scenario were maintained indefinitely, but it would be stable if the two phases alternated in time (*cf.* Huenneke and Marks 1987, Moloney 1988).

In this study, we constructed size-classified matrix population models (Lefkovitch 1965, Caswell 1989) based on observed patterns of recruitment, growth, and survival of *Fagus grandifolia* in Woodyard Hammock, an old-growth forest in northern Florida, over a 14 year period that included Hurricane Kate in 1985. We used asymptotic population growth rates projected with our matrix models to evaluate the four hypotheses of population persistence. By denoting λo and λc, the asymptotic population growth rates for the "open" and the "closed" canopy phases respectively, our hypotheses become: H1 (resistance), $\lambda o = \lambda c = 1$; H2 (recovery), $\lambda o < 1 < \lambda c$; H3 (release) $\lambda o > 1 > \lambda c$; and H4 (complementation) $\lambda o < 1, \lambda c < 1$. All these hypotheses were subjected to the assumption that the population is persistent under a natural long-term sequence of "open" and "closed" canopy phases. We tested this assumption by simulating long-term sequences of "open" and "closed" canopy phases with sequences of transition matrices. From our demographic perspective, we analyzed trends in population size and structure, rather than in relative abundance in the community, and we did not discriminate between the interactions with abiotic factors and with co-occurring species.

METHODS

Study Area

Woodyard Hammock is a 30 ha Southern Mixed Hardwood Forest located at Tall Timbers Research Station, 32 km north of Tallahassee, in Leon County, northern Florida, at 30°35'N and 84°20'W (Blaisdell et al. 1974, Hirsh 1981, Platt and Hermann 1986, Platt and Schwartz 1990). The forest is situated just inland from the northern shore of Lake Iamonia, at about 40 m above the sea level, on level terrain comprised of clay soils developed from marine deposits exposed during the Miocene (Platt and Schwartz 1990). According to records of two weather stations located near Woodyard Hammock (Quincy and Monticello, Florida), the mean annual temperature is 19 ^{0}C, with a maximum monthly mean of 27 ^{0}C in July and a minimum of 11 ^{0}C in January, the mean annual rainfall is 1420 mm, and the driest months are October and November with a monthly mean of 70 mm (NOAA 1982). The growing season is about 273 days long, from March through November (Canham et al. 1990). According to NOAA records (Jarvinen et al. 1984), between 1886 and 1992, four storms with maximum sustained windspeeds over 100 km/h passed within 100 km of Woodyard Hammock, in 1886,1894,1941, and 1985. The last of these storms, Hurricane Kate, passed within 30 km of Woodyard Hammock on November 21, 1985, following a period of heavy rainfall that had saturated the soil. Downbursts of wind up to 160 km/h were recorded in Leon County during the hurricane (Clark 1986) and tropical storm force winds lasted for about eight hours.

A 4.5 ha study plot was established in the middle of Woodyard Hammock in 1978 (Hirsh 1981, Platt and Hermann 1986). All trees in the plot with

diameter at 1.5 m height (dbh) equal to or greater than 2 cm were measured for dbh, classified as overstory (>15 m tall) or understory (≤15 m tall), mapped and tagged. Censuses were repeated biennially to record diameter growth and recruitment of trees in the entire plot. Stems that grew into the dbh ≥ 2 cm size class were recorded as recruits unless there were evident connections to root systems of other trees. Mortality was recorded annually until 1985 and biennially starting in 1986.

Fagus grandifolia was one of the dominant overstory species in the plot. In 1978, density of this species was 124 trees/ha (dbh ≥ 2 cm) and basal area was 7.6 m^2/ha. The number of live *F. grandifolia* individuals (dbh ≥ 2 cm) in the plot varied between 575 in 1978 and 546 in 1992. Our data base contains records for 641 trees of this species. Between 1978 and 1992, the population of *F. grandifolia* represented between 23 and 28 % of all trees (dbh ≥ 2 cm) of overstory species in the plot. Other dominant overstory species were *Magnolia grandiflora* (density=64 trees/ha, basal area=24.7 m^2/ha), *Liquidambar styraciflua* (124 trees/ha, 4.2 m^2/ha) and *Pinus glabra* (40 trees/ha, 4.4 m^2/ha). The three most abundant understory species were *Ostrya virginiana*, *Carpinus caroliniana*, and *Ilex opaca*. Gaps, defined as openings in the overstory, were mapped as polygons formed by connecting the bases of the bordering trees (i.e. expanded gaps of Runkle 1982). These expanded gaps occupied 31% of the plot before, and 62% after Hurricane Kate (Batista and Platt 1996). In 1992, the gap area remained increased partly as a consequence of delayed mortality of damaged canopy trees.

Our analysis is based on the data obtained between 1978 and 1992. Consequently, the data set encompasses seven years preceding and seven

years following Hurricane Kate. Climatograms (Walter 1971), constructed with data from weather stations located near Woodyard Hammock revealed no striking differences between the patterns of monthly rainfall and mean temperature of these two seven year periods.

Analysis of demographic patterns

In the first part of our analysis we examined changes in the probability distribution of tree dbh, in the rate of recruitment, and in individual growth and mortality patterns of *Fagus grandifolia* associated with the occurrence of Hurricane Kate in 1985. The period between 1978 and 1984 was assumed to represent a "closed" canopy phase, and the period 1984-1992 an "open" canopy phase of our conceptual model. Note that our use of the terms "open" and "closed" is relative, as the gap area was substantial before Hurricane Kate.

Probability distribution of tree size.- The Weibull distribution (Antle and Wain 1988) was fitted to each of the empirical dbh probability distributions obtained from the censuses. The parameters were estimated by maximum likelihood and the goodness of fit was assessed using the Kolmogorov-Smirnov one sample test (Daniel 1990).

Recruitment.- Observed number of individuals reaching 2 cm dbh between two consecutive censuses were compiled from the data base. The hypothesis of equal recruitment (number of recruits) among the two-year intervals ("constant" recruitment rate) was tested with the Pearson chi-square statistic (Agresti 1990).

Growth.- A simple linear regression model of the form $d = a + b\,x + e$, where d is the increment, x is the initial dbh, a and b are regression parameters, and e is an error term, was fitted to individual dbh increments between 1978

and 1984 ("closed" canopy). For the increments from 1984 to 1992 ("open" canopy), a segmented regression model of the form $d = a + b\,x + e$, for $x<x_t$ and $d = z + e$, for $x \geq x_t$, was fitted, where z is a plateau attained by the expected increment at the threshold dbh $x_t = (z-a)/b$. Lack of noticeable trends in the residuals when plotted against initial dbh and against predicted growth was the criterion for choosing these models. The parameters were estimated by least squares; for the segmented model the sum of squared errors was minimized by the Gauss-Newton method. To facilitate comparing between periods, after these analyses, we obtained mean annual growth rates dividing the increments by the corresponding interval length. In addition, differences in mean annual growth rate between periods for selected dbh classes were examined with a *t*-test calculated taking into account the partially paired structure of the data.

Mortality.- Logistic regression (Agresti 1990) was applied to model individual tree death as a Bernoulli variable $m(x)$ that takes the value 1 if the tree is dead at the end of the period considered, where x is the dbh. The probability of death $\pi(x)$ varied according to $ln\{\pi(x)/(1-\pi(x))\} = p\{ln(x)\}$, where $p\{\eta\}$ denotes a complete polynomial in η. We fitted models with quadratic polynomials for the interval 1978-84 ("closed" canopy) and for the immediate mortality caused by Hurricane Kate, and with a cubic polynomial for the intervals 1984-92 ("open" canopy) and 1986-92 (strictly post-hurricane mortality). A survival function was derived from these models as $s(x) = 1 - m(x)$, which takes the value 1 with probability $\sigma(x) = 1 - \pi(x) = \{1+exp[p(ln(x))]\}^{-1}$. For comparison, average annual mortalities were derived for the 1978-84 and 1986-92 intervals as $1 - \sigma(x)^{1/6}$.

Matrix models

In the second part of the analysis, we integrated the observed demographic patterns in size-classified matrix population models (Caswell 1989). We constructed separate transition matrices for the "closed" and the "open" canopy phases. Vital rates included in these matrices were estimated over the 1978-84 and the 1984-92 intervals respectively, so that the projection intervals were of 6 years for the "closed" and of 8 years for the "open" canopy models. We projected asymptotic population growth rates and stable size frequency distributions for both phases, and we examined the sensitivity of asymptotic population growth to small changes in the vital rates. In addition, we manipulated the matrices to simulate the long-term dynamics of the population under various hurricane frequencies, as well as the effects of large changes in selected vital rates, and of isolating changes in vital rates that in fact occurred simultaneously with other changes (e.g. changes in growth and in mortality). Transition probabilities in each of these models were not varied with density. For this reason, the results of the analyses are not predictions but projections that describe the population behavior over our observation periods (see Caswell 1989).

Estimation of the transition matrices.- We assumed that the only life-cycle transitions that could occur in one projection interval were death, survival in the same size class, survival and growth to the next size class, and reproduction. Consequently, non-zero elements of the transition matrices were restricted to the diagonal, the first sub-diagonal and the first row. We denote $A = \{a_{ij}\}$ a transition matrix, with diagonal elements $a_{ii} = P_i$, $(i = 1,...,k)$, first sub-diagonal elements $a_{i+1,i} = G_i$, $(i = 1,...,k-1)$, and first row elements $a_{1i} = F_i$,

(i = 2,...,k), where k is the number of size classes. In what follows, we omit the subindices in P, G and F whenever we refer to a generic size class with lower limit *L* and upper limit *U*. The true values of these parameters are,

$$P = Prob.\ \{L \le y < U \text{ and } s(x)=1 \mid L \le x < U\},$$

$$G = Prob.\ \{U \le y \text{ and } s(x)=1 \mid L \le x < U\}, \text{ and}$$

$$F = E\ \{\text{number of recruits produced} \mid L \le x < U\},$$

where *x* and *y* respectively denote the dbh at the beginning and at the end of the projection interval, and *s(x) = 1* indicates survival. We estimated these vital rates based on the fitted size-probability distribution, growth and mortality curves, rather than on observed transition frequencies. The appeal of this approach is that the estimators change smoothly with changes in the size-class boundaries. Provided the fitted models are correct, our estimators have the same essential large sample properties as those based on observed frequencies (Agresti 1990).

In our growth regression models $y = g(x) + e$, where $g(x) = x + E\{d\}$. When the variance of *e* is small relative to the width of the size class, a good approximation of P, the probability of survival in the same class, is given by,

$$P^* = Prob.\ \{L \le g(x) < U \text{ and } s(x)=1 \mid L \le x < U\}$$

$$= \{\int_{(L,\,q)} f(x)\ \sigma(x)dx\} \div \{\int_{(L,\,U)} f(x)\ dx\}, \qquad (1)$$

were *s(x)* equals *1* with probability $\sigma(x)$, $q = \max[L, g^{-1}(U)]$ and *f(x)* is the probability density function of the initial dbh. We estimated P by replacing *q*, *f(x)*, and $\sigma(x)$ in (1) by their estimates based on the growth, Weibull probability distribution, and mortality models respectively. Similarly, we approximated G, the probability of survival and growth to the next class, with,

$$G^{*} = \text{Prob}\{U \le g(x) \text{ and } s(x)=1 / L \le x < U\}$$
$$= \{\int_{(q,U)} f(x)\, \sigma(x) dx\} \div \{\int_{(L,U)} f(x)\, dx\}, \quad (2)$$

and constructed the estimate using the estimated growth, probability distribution, and mortality models. In other words, with $g^{-1}(U) > L$, our estimator of P was the predicted proportion of trees with initial size between L and $g^{-1}(U)$ that survive to the end of one projection interval, out of all trees with initial size between L and U; and our estimator of G was the predicted proportion of surviving trees with initial size between $g^{-1}(U)$ and U, out of the same total (Note that if $q = L$ then $P^{*} = 0$). In addition, we calculated the estimators of $\Sigma_i = P_i + G_i$, the total survival rate of individuals in the i^{th} class at the beginning of the projection interval, and of $\Gamma_i = G_i / (P_i + G_i)$, the conditional probability of growth to the next class for surviving individuals.

Estimation of fecundity was based on observed recruitment (as defined above), with the simplifying assumptions that only overstory individuals reproduce (cf. Harcombe et al. 1982), and that all overstory individuals have equal expected reproductive output (cf. Enright and Ogden 1979). Accordingly, our estimator of F was: $F^{*} = (n \div O)\, c$, where n is the number of recruits alive at the end of the period under consideration, O is the number of overstory individuals present at the beginning of this period, and c is the expected proportion of overstory individuals in the size class. This proportion was set to $c = 0$ for size classes below 16 cm, and to $c = \{\int_{(L,U)} f(x)\, h(x)\, dx\} \div \{\int_{(L,U)} f(x)\, dx\}$ otherwise, where $h(x)$ is the probability that an individual with dbh = x is in the overstory as estimated by a logistic regression model (Agresti 1990) on a linear function of x. Lacking of actual fecundity data, we chose this crude approach

because it involved few assumptions. The models, in turn, proved to be very robust to differences in estimated fecundities (cf. Harcombe 1987).

Definition of the size classes.- We delimited the size classes using a procedure designed to find a compromise between two types of error described by Vandermeer (1978) and Moloney (1986). The approximations of P and G from equations (1) and (2) improve, for a given variance of e, as the width of the size class increases. The error in this approximation corresponds to Vandermeer's (1978) "error of estimation", which decreases as the size-class width increases. A second type of error is introduced when using the transition matrix to project the size-class distribution in time because all individuals in the same size class are implicitly assigned identical transition probabilities. This is Vandermeer's (1978) "error of distribution", which decreases as the size-class width decreases below a finite value, provided the individual transition probabilities are continuous functions of size. The two errors are simultaneously introduced when estimates $\hat{P}$ of P, and $\hat{G}$ of G, are calculated from the equations (1) and (2), setting $f(x)$ to a uniform distribution function (i.e. $f(x) = 1/(U-L)$, $L \leq x < U$, and $f(x) = 0$ otherwise). We defined the global quadratic error as $\epsilon = [(\hat{P} - P) / P]^2 + [(\hat{G} - G) / G]^2$, and estimated this error by replacing in the formula the true P and G with the corresponding observed transition probabilities.

The criterion used to set the size-class boundaries was the sum of global quadratic errors estimated for the 1978-84 and 1984-92 intervals. We started with the smallest size-class by setting L = 2 cm and computing the sum of errors for increasing values of U. The upper limit of this class was set to the value of U for which the sum of errors appeared to have the absolute minimum in a graph

(cf. Moloney 1986). This procedure was repeated for successive size-classes by setting the lower limit to the value of the previous-class upper limit (all classes were defined by intervals closed to the left and open to the right). The resulting size classes were 2-4, 4-6, 6-11, 11-16, 16-28, 28-40, 40-52, 52-64, and > 64 cm dbh. Beyond 64 cm dbh, observed transition probabilities became unreliable because the number of individuals was small.

Eigenanalysis and sensitivity analysis.– The dominant eigenvalue λ and the corresponding left eigenvector $\boldsymbol{v}$ and right eigenvector $\boldsymbol{w}$ of each transition matrix were obtained by the power method (Caswell 1989). These eigenvalues give the limit approached by the finite population growth rate if the transition frequencies remained constant. To compare between phases, these asymptotic growth rates were transformed to an annual basis by raising the λ's to the inverse of the corresponding projection interval in years (6 for 1978-84, and 8 for 1984-92). The stable size-class distribution associated with each transition matrix was given by its first right eigenvector $\boldsymbol{w}$ scaled so that its elements added to 1.

Elasticities of λ with respect to the non-zero elements of the transition matrices were calculated as $\xi(a_{ij}) = \delta ln(\lambda)/\delta ln(a_{ij}) = a_{ij}\, v_i\, w_j / (\lambda \boldsymbol{v'w})$, where v_i and w_j are respectively the i^{th} and j^{th} element of the eigenvectors $\boldsymbol{v}$ and $\boldsymbol{w}$ (Caswell 1989). These functions measure the proportional change in λ resulting from a small proportional change in a_{ij} when all other components of the model are fixed. de Kroon et al. (1986) noted that, since $\lambda = \boldsymbol{v}' A \boldsymbol{w} / \boldsymbol{v'w} = \sum_{ij} a_{ij} v_i w_j / \boldsymbol{v'w}$, each elasticity can be regarded as the relative contribution to λ of the corresponding matrix element. Sums of these contributions were computed for the diagonal, for the subdiagonal, and for the fecundity elements

of the transition matrices (cf. Enright and Watson 1991, Gotelli 1991). Each of these sums measures the proportional change in λ resulting from a small proportional change common to all the P_i, G_i, or F_i respectively, when the rest of the matrix is fixed. In addition, we computed the contribution to λ of Σ_i, the total survival rate of individuals in the i^{th} size class. In our case, it is straightforward that $\xi(\Sigma_i) = \xi(P_i) + \xi(G_i)$, (by using equations 4.60, 4.61, 6.49 and 6.38 from Caswell 1989).

Overall sensitivities of λ to small changes in the non-zero elements of the transition matrices were calculated as,

$$S = \{\sum_i(\delta\lambda/\delta P_i)^2 + \sum_i(\delta\lambda/\delta G_i)^2 + \sum_i(\delta\lambda/\delta F_i)^2\}^{1/2},$$

where the summations are taken over the transition-matrix elements not set to zero a priori. This measure is an upper bound to the change in λ produced by a given small perturbation of the transition matrix (Caswell 1978, 1989). In addition, sensitivities of λ to large departures from observed recruitment and mortality rates were examined numerically by recalculating λ after suitable alterations of the elements in the transition matrix.

Bootstrap comparisons.– We used a bootstrap procedure (Efron and Tibshirani 1993) to construct confidence intervals for estimated eigenvalues, eigenvectors, sensitivities, elasticities, and for the difference between annual finite population growth rates projected from the 1978-84 and 1984-92 intervals. We generated 1000 bootstrap samples by, each time, drawing randomly and with replacement 641 trees from our data base (cf. Meyer et al. 1986). The same analysis performed with the original data set ("all data") was repeated for each bootstrap sample. This yielded new estimates for the parameters of the 1978 and 1984 Weibull distributions of dbh, and for the parameters of the

growth and mortality regression models for the 1978-84 and 1984-92 intervals. These estimates were used to construct a transition matrix for each period in the same way as for "all data". Eigenanalysis and sensitivity analysis of these two matrices were performed (leading eigenvectors were always written with non-negative elements), and the difference between population growth rates projected from them was computed after transformation to an annual basis. For each statistic, we defined the 1-2α confidence interval as limited by the α and 1-α percentiles of the corresponding probability distribution generated by the 1000 bootstrap samples (i.e. the "percentile intervals", Efron and Tibshirani 1993). Due to our resampling scheme these confidence intervals account for the covariance between elements in the transition matrices. We chose this computer intensive approach, instead of the analytic method proposed by Alvarez-Buylla and Slatkin (1993), because it required no assumption about a parametric distribution for the transition matrices, and straightforwardly produced confidence intervals for statistics other than λ. As the original sample is not strictly random, we regard the results of this resampling procedure as our best approximation to the error of the estimates (see Caswell 1989, p. 185).

Software.- The t-tests for comparing growth rate between periods and the χ^2 test of constant recruitment rate were calculated manually. All other statistical models were fitted using SAS: Proc LIFEREG for Weibull distributions, Proc REG and NLIN for growth models, and Proc LOGISTIC for mortality models (SAS Institute Inc. 1989b). The estimation and analysis of transition matrices was programmed in the SAS Interactive Matrix Language (SAS Institute Inc. 1989a). For the original data, and for the generation and analysis of bootstrap samples, this program was combined with SAS code for

sorting the data and for fitting the statistical models using the SAS Macro Processing facility (SAS Institute Inc. 1990).

RESULTS

Observed demographic patterns

Density and size probability distribution.- Between 1978 and 1992 the density of *Fagus grandifolia* (dbh ≥ 2 cm) in the Woodyard Hammock plot remained between 128 and 121 individuals/ha (Figure 3.1). The probability distribution of dbh (≥ 2 cm) was inverted-J shaped, and the largest observed dbh values were between 83.0 and 94.5 cm. The empirical distributions observed in 1978, 1984, 1986 and 1992 fit to Weibull distributions. Kolmogorov-Smirnov goodness-of-fit tests did not reject the hypothesis with $\alpha = 0.1$ for 1978, 1986 and 1992, and with $\alpha = 0.05$ for 1984 (Table 3.2). All trees smaller than 16 cm dbh were in the understory (≤ 15 m tall), and all trees larger than 64 cm dbh were in the overstory (> 15 m tall).

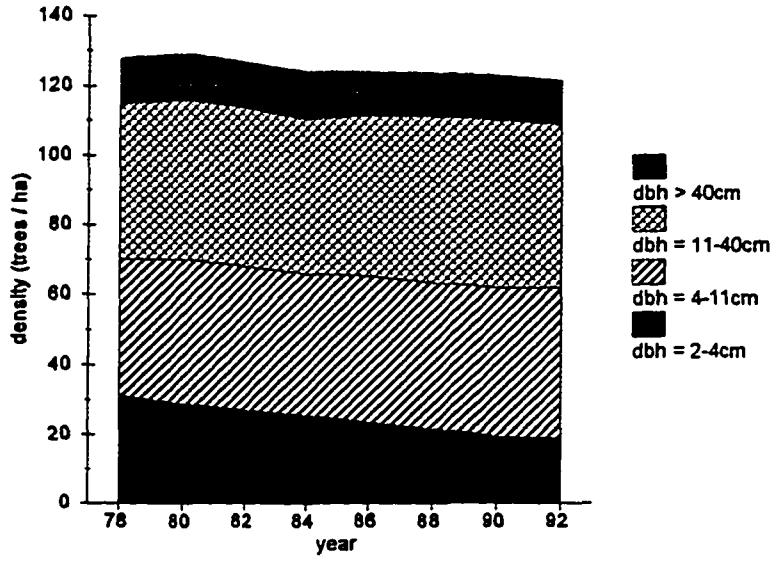

FIGURE 3.1. Changes in *Fagus grandifolia* density between 1978 and 1992 in a 4.5 ha plot of Southern Mixed Hardwood Forest in Woodyard Hammock, Florida.

TABLE 3.2. Fitted Weibull distributions of tree dbh. N = Number of trees, α and γ parameters of the Weibull distribution with c.d.f. $F(x) = 1 - exp\{-\alpha(x-2)^{\gamma}\}$, D = Kolmogorov-Smirnov one-sample, two-sided test statistic, P = null probability of a larger D.

Year	N	α	γ	D	P
1978	575	0.142	0.782	.044	>0.1
1984	558	0.121	0.823	.057	>0.05
1986	555	0.126	0.815	.038	>0.1
1992	546	0.120	0.816	.043	>0.1

Recruitment.- The number of recruits of *Fagus grandifolia* in the plot varied between 3 and 17 per two-year period. All these recruits were derived from seeds (see Poulson and Platt 1995 for methods of determining the seed or sprout origin). Although recruitment was quite variable among two-year periods (C.V. = 0.47), the hypothesis of constant recruitment rate over the 1978-92 period was not rejected by a χ^2 test with $\alpha = 0.05$ ($\chi^2 = 12.5$, d.f. = 6). Under this hypothesis the estimated recruitment rate was 1.06 trees.ha^{-1}.yr^{-1}. No trend in recruitment over time was noticeable ($P = 0.80$).

Growth.- Diametral growth rate of *Fagus grandifolia* increased with tree dbh. In the 1978-84 interval ("closed" canopy), increase in tree growth rate with dbh fit to a linear model, varying from about 1 mm/yr for the smallest trees to about 6 mm/yr for the largest (Figure 3.2a). Dispersion about the linear trend was substantial (standard error = 1.1 mm/yr), and growth of individual trees ranged from non-detectable over the whole period to about 8 mm/yr. In the 1984-92 ("open" canopy) interval, the relation between tree growth and dbh was

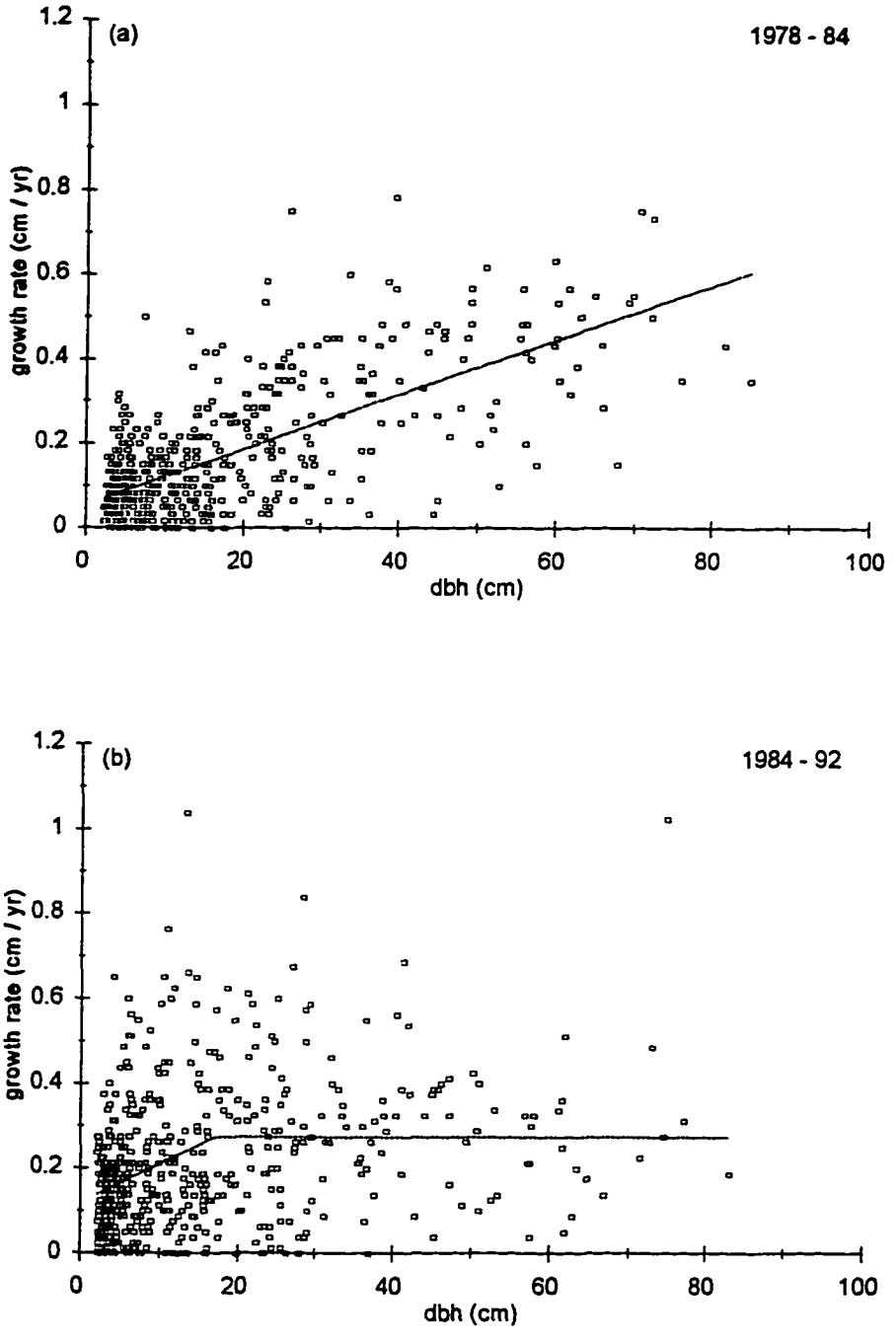

FIGURE 3.2. Association between diametral growth of *Fagus grandifolia* and dbh in a 4.5 ha plot in Woodyard Hammock, Florida. (a) 1978-84; (b) 1984-92.

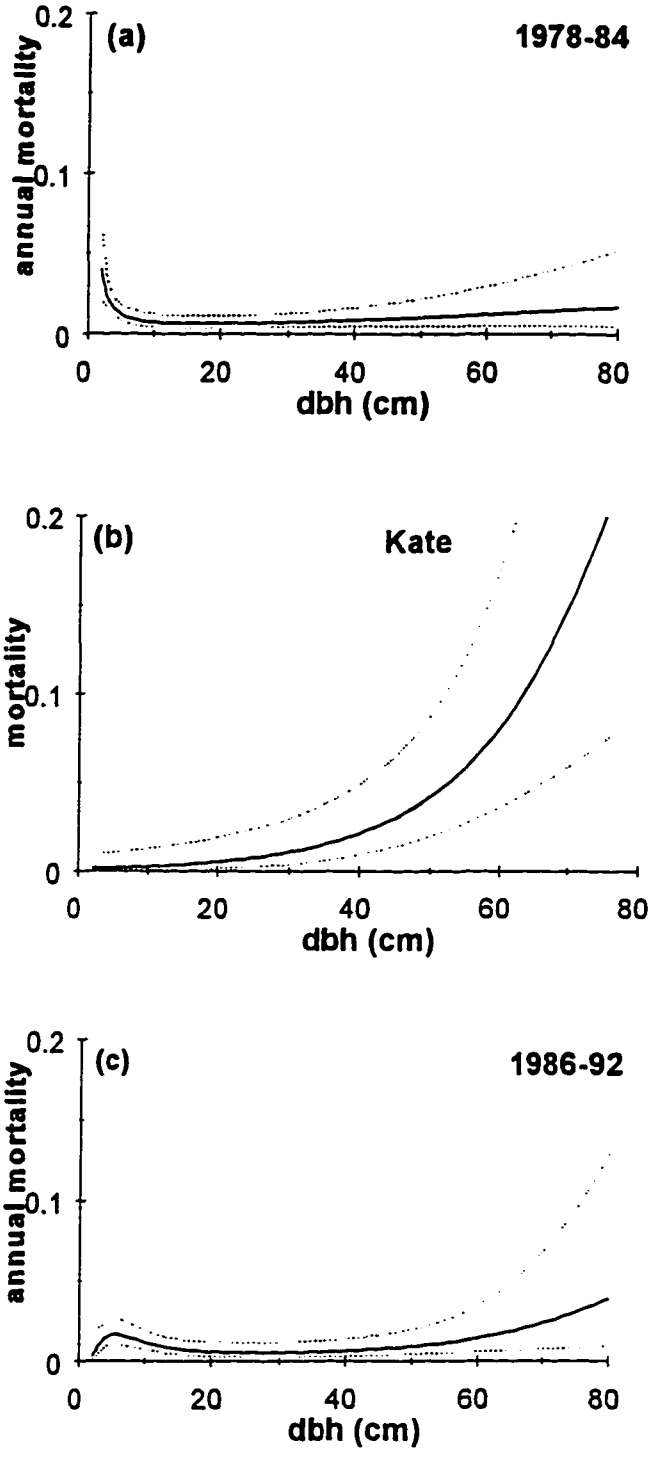

FIGURE 3.3. Logistic regression curves of expected mortality of *Fagus grandifolia* as a function of tree dbh, dotted lines enclose the 95% confidence intervals for the expected mortality. a) 1978-84; b) period 1985; c) 1986-92.

no longer linear, but fitted a segmented model predicting increased growth with tree dbh for trees smaller than 17 cm dbh, but no trend for larger trees (Figure 3.2b). Dispersion about this line (*s.e.* = 1.6 mm/yr) was larger than for the 1978-84 period and growth of individual trees ranged from non-detectable over the whole period to about 10 mm/yr. The *t*-tests ($\alpha = 0.05$) for comparing mean annual diametral growth in each size class between the 1978-84 and 1984-92 periods detected a significant increase in growth rate of small trees (size classes 2-4, 4-6, and 6-11, 11-16 cm dbh), a significant decrease in growth rate of trees 52 - 64 cm dbh, and no significant change in the remaining size classes.

Mortality.- In the 1978-84 ("closed" canopy) interval, mortality of *Fagus grandifolia* exhibited a U-shaped pattern of association with log-diameter of trees. Mortality predicted by the logistic regression model was maximum for the smallest trees, decreased rapidly with increasing dbh for trees smaller than 17 cm, and apparently increased with dbh for larger trees, although the error of estimation of large-tree mortality was high (Figure 3.3a). Immediate mortality caused by Hurricane Kate was significantly higher than the 1978-84 average annual mortality for trees larger than 40 cm dbh, but not for smaller trees (Figure 3.3b). Following the hurricane the mortality of trees 2 - 4 cm dbh decreased significantly (Figure 3.3c). As a result, the combined pattern for 1984-92 ("open" canopy period) was not U-shaped, with the mortality being significantly lower than in the "closed" canopy period for the smallest trees (2-4 cm dbh), significantly higher for trees larger than 64 cm dbh, and not significantly different for medium-sized trees.

Matrix models

"Closed" canopy phase.– Estimated probabilities along the diagonal of the 1978-84 transition matrix were higher than along the sub-diagonal (Table 3.3), reflecting the greater probabilities that surviving trees would remain in the same size class than grow into the next size class. Total survival rates (Σ) implicit in the transition matrix were compatible with the mortality patterns shown in Figure 3.3a. The leading eigenvalue of this matrix (Table 3.4) was < 1, projecting a slight decline in population size. However, as the value λ =1

TABLE 3.3. Estimated transition matrix for the *Fagus grandifolia* population in Woodyard Hammock, Florida, in the interval 1978-84; dbh classes are in cm, Σ are the tree survival rates for each dbh class, and Γ are probabilities of growth to the next class implicit in each transition matrix.

dbh	2-4	4-6	6-11	11-16	16-28	28-40	40-52	52-64	64-
2-4	0.6955	0	0	0	0.0429	0.1488	0.2289	0.2471	0.2498
4-6	0.1575	0.6938	0	0	0	0	0	0	0
6-11	0	0.2321	0.8358	0	0	0	0	0	0
11-16	0	0	0.1139	0.8065	0	0	0	0	0
16-28	0	0	0	0.1526	0.8826	0	0	0	0
28-40	0	0	0	0	0.0768	0.8444	0	0	0
40-52	0	0	0	0	0	0.1085	0.8032	0	0
52-64	0	0	0	0	0	0	0.1396	0.7603	0
64-	0	0	0	0	0	0	0	0.1701	0.8878
Σ	0.8530	0.9259	0.9497	0.9591	0.9594	0.9529	0.9428	0.9304	0.8878
Γ	0.1847	0.2507	0.1200	0.1591	0.0801	0.1139	0.1480	0.1828	

TABLE 3.4. Asymptotic population growth rates projected with the transition matrices estimated for the "closed" (1978-84) and "open" canopy (1984-92) phases. λ, asymptotic growth rates scaled as the original projection intervals; Annual basis, transformed as $\lambda^{1/\Delta}$, where Δ is the projection interval in years. Relative contributions to λ of the rates of survival in the same size class P, rates of survival with growth to the next class G, and fecundity rates F. Values in parenthesis are limits of the bootstrap 95% confidence intervals.

Period	λ	Annual	Elasticity analysis (contributions)		
		basis	P	G	F
1978-84	0.9834	0.9972	0.8328	0.1440	0.0232
	(0.9595,1.0123)	(0.9931,1.0020)	(0.8216,0.8906)	(0.0957,0.1525)	(0.0133,0.0263)
1984-92	1.0073	1.0009	0.7067	0.2492	0.0441
	(0.9785,1.0350)	(0.9973,1.0043)	(0.6847,0.7320)	(0.2281,0.2672)	(0.0396,0.0482)

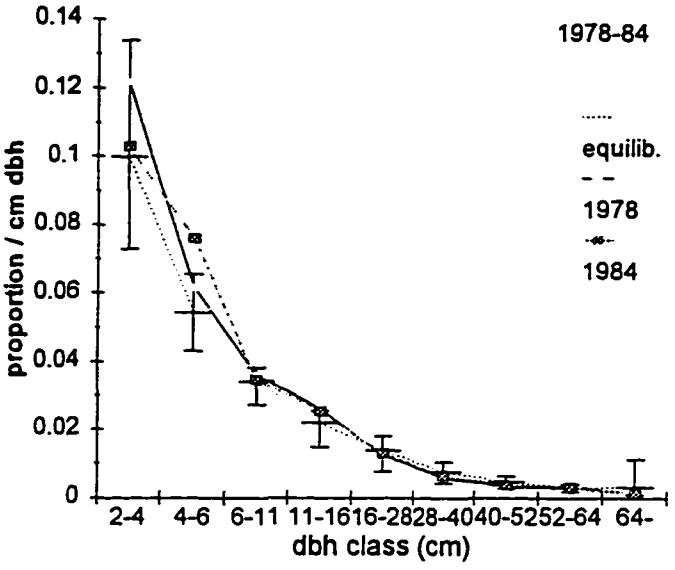

FIGURE 3.4. Stable size-class distribution of *Fagus grandifolia* projected for the 1978-84 interval, and size-class distributions observed in 1978 and 1984. Bars enclose the 0.95 bootstrap confidence intervals for the stable frequencies.

corresponded to percentile 84.2 of the bootstrap probability distribution, the hypothesis of $\lambda = 1$ or limiting population-size stability was not rejected ($P = 0.316$). The stable size-frequency distribution for this period was monotonic decreasing, resembling the general pattern of the empirical distributions from 1978 and 1984 (Figure 3.4). However, in a few of the size classes, the observed frequencies fell outside the 95% bootstrap confidence intervals for the equilibrium probabilities.

The overall sensitivity of λ to changes in the non-zero elements of the transition matrix was $S = 0.574$, with 95% confidence interval boundaries at 0.527 and 0.612. The elasticities of λ with respect to all diagonal elements p_i were significantly higher than the elasticities with respect to the corresponding sub-diagonal elements g_i, and these were usually significantly higher than the

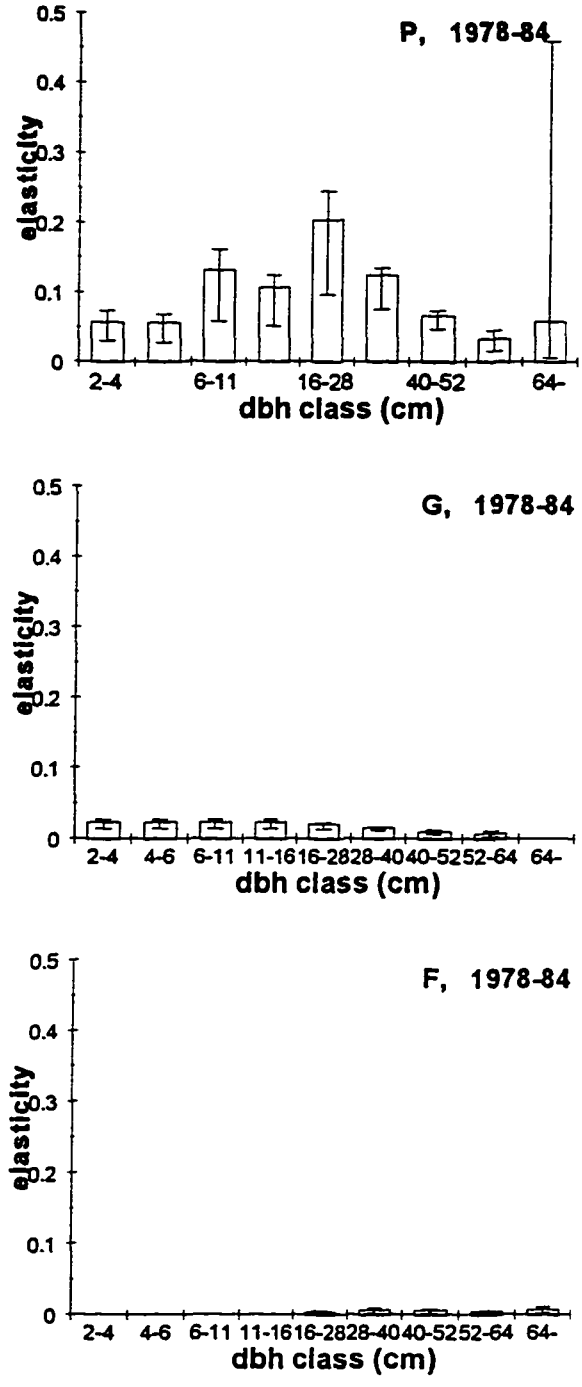

FIGURE 3.5. Elasticities of the first eigenvalue of the 1978-84 transition matrix (asymptotic finite population growth rate) respect to: survival probabilities of trees in the same size class (P), probabilities of survival and growth to the next size class (G), and mean fecundity per tree in each size class (F). Bars enclose the 0.95 bootstrap confidence intervals.

TABLE 3.5. Estimated transition matrices for the *Fagus grandifolia* population in Woodyard Hammock, Florida, in the interval 1984-92; dbh classes are in cm. Σ are the tree survival rates for each dbh class, and Γ are probabilities of growth to the next class implicit in each transition matrix.

dbh	2-4	4-6	6-11	11-16	16-28	28-40	40-52	52-64	64-
2-4	0.4739	0	0	0	0.0610	0.2265	0.3759	0.4158	0.4223
4-6	0.4341	0.3259	0	0	0	0	0	0	0
6-11	0	0.5399	0.6455	0	0	0	0	0	0
11-16	0	0	0.2550	0.6088	0	0	0	0	0
16-28	0	0	0	0.3311	0.8332	0	0	0	0
28-40	0	0	0	0	0.1234	0.8249	0	0	0
40-52	0	0	0	0	0	0.1266	0.7968	0	0
52-64	0	0	0	0	0	0	0.1233	0.7372	0
64-	0	0	0	0	0	0	0	0.1119	0.4929
Σ	0.9080	0.8658	0.9005	0.9399	0.9566	0.9515	0.9201	0.8491	0.4929
Γ	0.4781	0.6236	0.2831	0.3523	0.1290	0.1330	0.1340	0.1318	

elasticities with respect to the fecundity elements F_i (Figure 3.5). Consequently, the total relative contribution to λ of the rates of survival in the same size class was significantly higher than that of the rates of survival and growth to the next class, which was significantly higher than the total contribution of fecundities (Table 3.4). The elasticities of λ with respect to the total survival rates Σ_i, and the elasticities with respect to the diagonal elements P_i, increased from the smallest to the 16 - 28 cm dbh class, then decreased with dbh for larger

classes. Estimation error of the elasticity of λ with respect to survival in the largest-tree size class was very large (Figure 3.5).

"Open" canopy phase.- Compared to the 1978-84 transition matrix, the 1984-92 matrix had lower probabilities along the diagonal, higher probabilities along the sub-diagonal, and slightly increased fecundities (Table 3.5). Although these differences result in part from the change in the projection interval, they also reflect changes in the patterns of average annual survival, growth, and recruitment. Total survival rates (Σ) changed for the small and for the large classes (increased in the 2-4 and decreased in the 4 - 16 cm and >40 cm dbh classes), but remained almost unchanged in the intermediate classes with respect to the 1978-84 matrix. The growth parameters (Γ) were higher than in the 1978-84 matrix for trees in smaller size classes, but lower for larger trees. These changes in Σ and Γ were compatible with the growth and mortality patterns depicted in Figures 3.3 and 3.4.

The leading eigenvalue of the estimated 1984-92 transition matrix exceeded 1, projecting a slight increase in population size (Table 3.4). However, as the value λ = 1 corresponded to percentile 30.3 of the bootstrap probability distribution, the hypothesis of λ = 1 or projected population-size stability was again not rejected (P = 0.606). The stable size-frequency distribution for this period was monotonic decreasing (Figure 3.6). Although the empirical distributions from 1984 and 1992 showed the same general pattern, many of the observed frequencies fell outside the 95% bootstrap confidence intervals for the corresponding equilibrium probabilities.

The difference between asymptotic growth rates estimated for the "open" and "closed" canopy phases, calculated after transforming the λ's to an annual

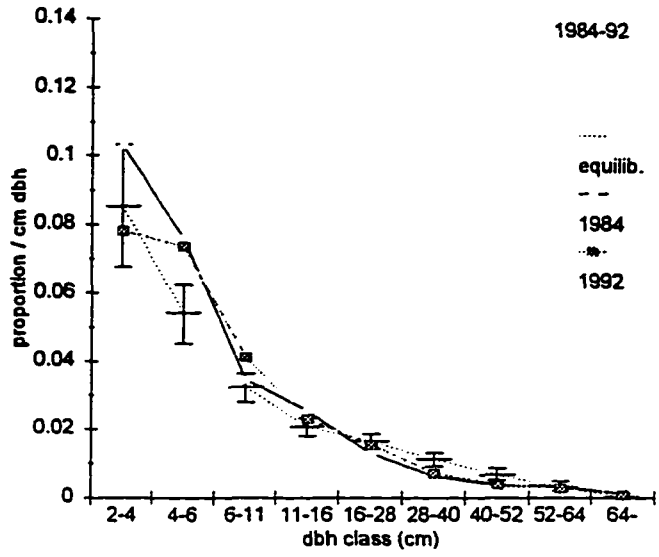

FIGURE 3.6. Stable size-class distribution of *Fagus grandifolia* projected for the 1984-92 interval, and size-class distributions observed in 1978 and in 1984. Bars enclose the 0.95 bootstrap confidence intervals for the stable frequencies.

basis, had 95% bootstrap confidence boundaries at -0.0026 and 0.0088. The value zero of this difference corresponded to percentile 14.7 of the bootstrap probability distribution, and therefore, the hypothesis of equal asymptotic population growth rate between the two phases was not rejected ($P = 0.294$). The stable size-frequency distributions projected from the 1978-84 and 1984-92 matrices had similar monotonic decreasing general pattern, but differed significantly in some of the frequencies (Figures 3.4 and 3.6).

The overall sensitivity of λ to changes in the 1984-92 transition matrix was $S = 0.619$ with 95% bootstrap confidence interval boundaries at 0.592 and 0.642. In this period, the elasticity of λ with respect to p_i was not significantly higher than with respect to g_i for the 2 - 4 cm dbh class, and significantly lower for the 4 - 6 cm dbh class. For classes of trees more than 6 cm dbh, the

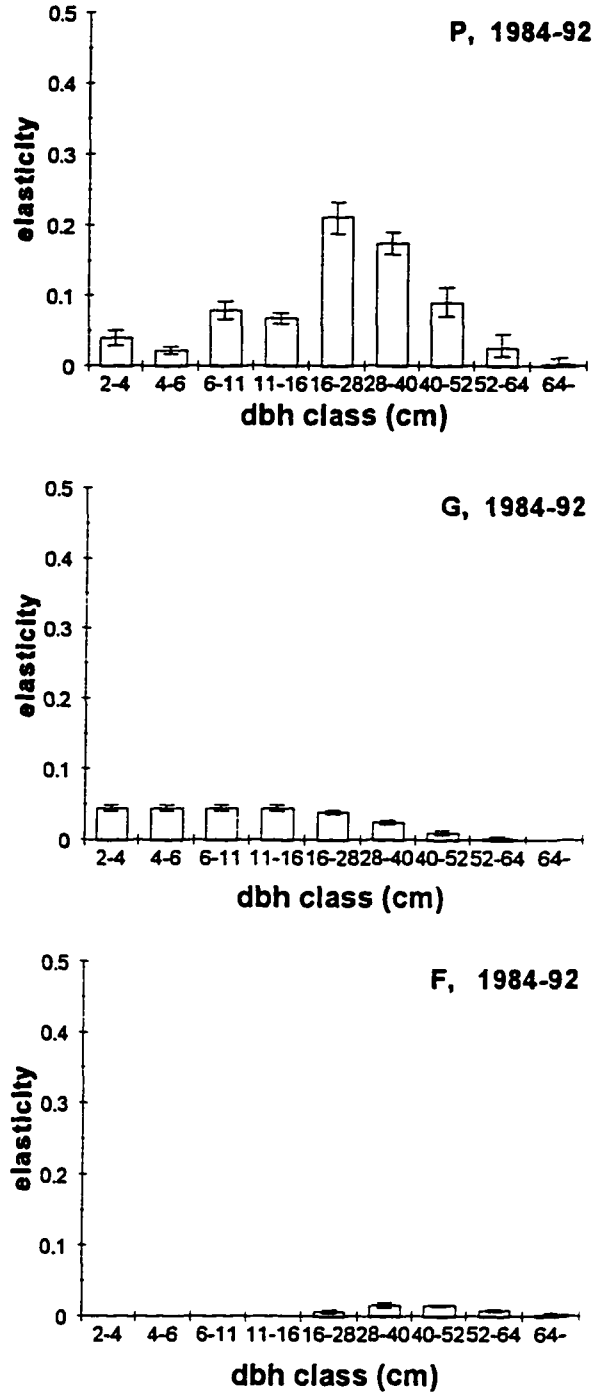

FIGURE 3.7. Elasticities of the first eigenvalue of the 1984-92 transition matrix (asymptotic finite population growth rate) respect to: survival probabilities of trees in the same size class (P), probabilities of survival and growth to the next size class (G), and mean fecundity per tree in each size class (F). Bars enclose the 0.95 bootstrap confidence intervals.

elasticities of λ with respect to P_i were significantly higher than those with respect to G_i and F_i (Figure 3.7). As for the "closed" canopy period, the total contribution to λ of the diagonal elements was larger than that of the sub-diagonal elements, and the latter was larger than the total contribution of fecundities (Table 3.4). There was, however, a significant shift in contribution from the diagonal elements to the sub-diagonal and fecundity elements between the 1978-84 and 1984-92 periods (Table 3.4). As in the "closed" canopy period, the elasticities of λ with respect to the total survival rates Σ_i, and with respect to the diagonal elements P_i, increased from the smallest to the 16 - 28 cm dbh class, and decreased with dbh for larger classes. The vital rates with highest contribution to λ were the survival probabilities in the 16 - 28 and 28 - 40 cm dbh classes.

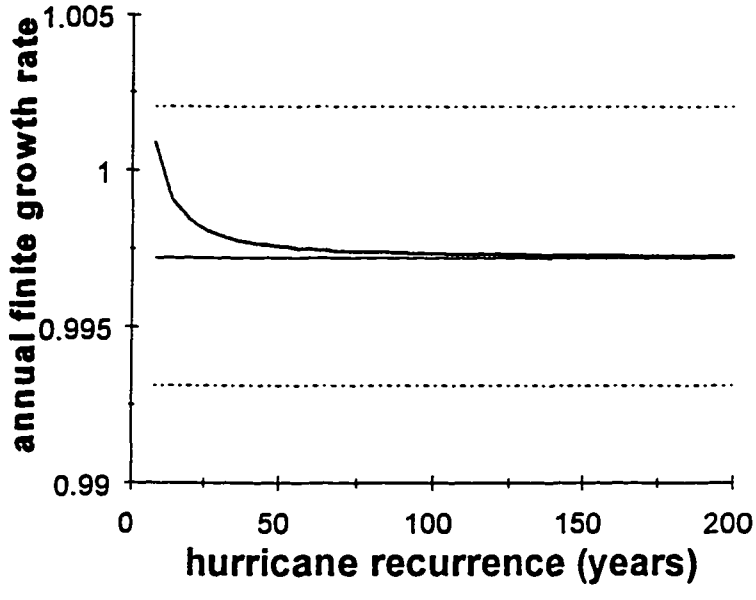

FIGURE 3.8. Asymptotic population growth rate projected by matrix models simulating varying hurricane recurrence times (Thick line). The horizontal thin line indicates the asymptotic growth rate projected from the 1978 - 84 interval and the dotted lines the corresponding 0.95 bootstrap confidence interval.

Simulation experiments.- We examined the long-term dynamics of the population under varying hurricane frequencies by constructing matrices $L(n) = A_c^n A_o$, where A_c and A_o are the transition matrices estimated for the "closed" and "open" canopy periods respectively (cf. Silva et al. 1991). In these simulations, n was adjusted so that the hurricane recurrence, $\rho = (8+6n)$ years, varied between 8 and 200 years. Asymptotic population growth rates were obtained by eigenanalysis of each matrix $L(n)$, and referred, for comparison, to an annual basis by raising each eigenvalue to the inverse of the corresponding ρ. In all simulations, the projected asymptotic growth rate was intermediate between the asymptotic growth rates projected for the 1978-84 and the 1984-92 transition matrices, approaching the "closed" canopy growth rate as the time between hurricanes increased (Figure 3.8). Since the hypotheses of population-size stability for these two periods, and the hypothesis of equal growth rate between periods were not rejected, this result suggested that the population size exhibits long-term stability under the simulated conditions. A drawback of these simulations was that the "open" canopy period was always set at the beginning of the sequence. To check for any bias due to this deterministic approach, we simulated stochastic sequences of "closed" and "open" canopy periods (cf. Bierzychudek 1982, Silva et al. 1991, Åberg 1992). Each sequence had 3000 matrices randomly drawn from the set $\{A_c, A_o\}$, with constant probabilities (i.e. homogeneous, independent environments, Caswell 1989). In the sequences, the probabilities of A_c and A_o were adjusted to simulate expected hurricane recurrence times between 10 and 200 years. Stochastic annual population growth rates were estimated as in Heyde and Cohen (1985) based on the last 2000 matrices of each sequence. These

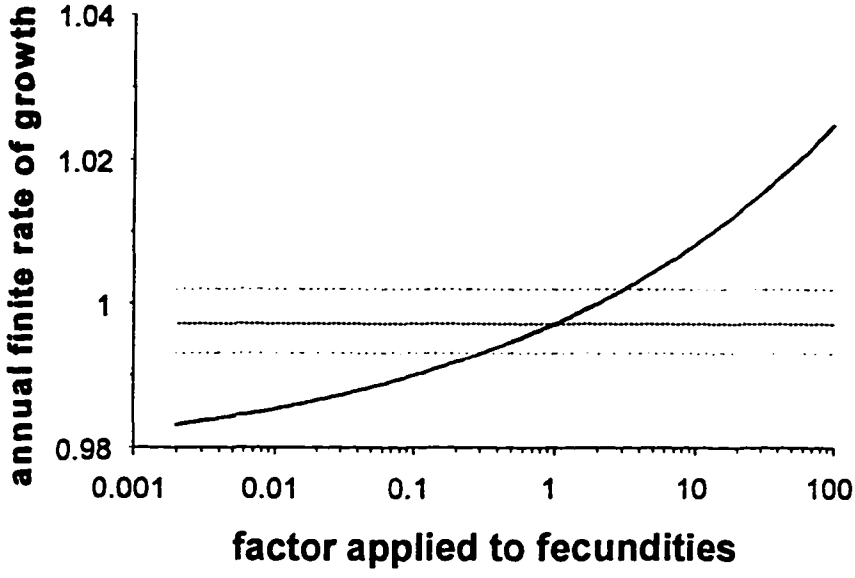

FIGURE 3.9. Simulated response of the asymptotic population growth to changes in the fecundity parameters F in the 1978 - 84 transition matrix. Dotted lines indicate the 0.95 bootstrap confidence interval for the asymptotic growth rate projected with the estimated fecundities.

estimates (not shown) closely overlapped those obtained with the deterministic approach, and fell within the 95% confidence interval for the asymptotic growth rate projected from the1978-84 matrix.

Responses to large departures from the recruitment rates observed in the "closed" canopy phase were simulated by multiplying all F values in the 1978-84 transition matrix by factors varying between 0.002 and 512. Asymptotic population growth rates projected from the perturbed matrices fell within the 95 % bootstrap confidence interval for the original rate when the factor was between 0.3 and 3 (Figure 3.9). Further increases or reductions of the F values produced significant changes in the growth rate. The largest simulated

reduction (0.002x) resulted in an annual growth rate of 0.9832, and the 512 fold increase in fecundity resulted in an annual growth rate of 1.0412.

TABLE 3.6. Eigenvalues obtained in simulation experiments isolating changes in vital rates from the "closed" to the "open" canopy periods. Effects are: M1, Decreased mortality in the 2-4 cm dbh class, M2, Increased mortality in the 4-16 cm dbh classes, M3. Increased mortality in the dbh ≥ 40 cm classes, G1, Increased growth in the 2-4 cm dbh class, G2, Increased growth in the 4-16 cm dbh classes, G3, Decreased growth in the dbh ≥ 40 cm classes, and F, increased recruitment rate.

Effect	λ
M3, G3	0.9794
M1, M2, M3	0.9810
none	0.9834
M2, G2	0.9849
F	0.9876
M1, G1	0.9944
G1, G2, G3	0.9987

The separate effects of changes in recruitment, survival, and growth patterns between the "closed" and the "open" canopy periods were isolated by altering selected elements of the 1978-84 transition matrix. Survival and growth changes were introduced in this matrix using appropriate values of Σ and/or Γ derived from the 1984-92 matrix to calculate new values for the corresponding P and G in the 1978-84 matrix as $P = (1 - .75\,\Gamma)\,\Sigma^{.75}$, and $G = .75\,\Gamma\,\Sigma^{.75}$ (the constant .75 was used to adjust to a 6 year interval). Recruitment rate differences were

introduced by replacing the F's with the corresponding values from the 1984-92 matrix multiplied by .75 to adjust to a 6 year interval. Both the changes in overall mortality, and in large tree growth and mortality, resulted in slightly decreased λ. The changes in overall growth and recruitment, as well as the changes in small tree growth and survival resulted in slightly increased λ (Table 3.6). However, all of these simulations produced eigenvalues within the 95 % bootstrap confidence interval of the original λ.

The effects of large increases in the mortality of the "open" canopy period (in large part hurricane mortality) were simulated by replacing selected diagonal, and the corresponding subdiagonal elements of the 1984-92 transition matrix by decreasing fractions of their original estimates. No decrease in the survival rates of trees larger than 40 cm dbh was sufficient to move the simulated λ outside the 95 % bootstrap confidence interval for the original λ. In contrast, the simulated λ fell below the lower limit of this confidence interval when the total survival rates in the 16 - 28 and 28 - 40 cm dbh classes were decreased by a factor of 0.85 or smaller, or when the survival rates of all trees more than 16 cm dbh were decreased by a factor of 0.89 or smaller.

DISCUSSION

Projections made from the observed demographic behavior of *Fagus grandifolia* in Woodyard Hammock indicate that this species would be persistent given the vital rates it exhibited during the 1978-92 period. Observed size and structure of the population changed very little over this period, and the asymptotic population growth rates were very close to λ=1 (stability) for all simulated long-term disturbance regimes. Transient departures from stability over the "closed" or "open" canopy periods are not likely to result in substantial

changes in population size. At the asymptotic rate of population growth estimated for the "closed" canopy phase, it to would take 248 years halve the population; and at the rate estimated for the "open" canopy phase, doubling the population would take 762 years.

The evidence from this study supports the resistance hypothesis. Although growth and mortality schedules of *Fagus grandifolia* changed as a result of Hurricane Kate in 1985, the asymptotic population growth rate did not change significantly, and did not depart significantly from $\lambda=1$ in either the "closed " or the "open" canopy periods. A pitfall in our result is that, while the resistance hypotheses is, in statistical terms, a null hypotheses, the power of the bootstrap tests we applied is unknown. However, this conclusion was consistent with the results of the elasticity analysis. Those vital rates making the largest contribution to λ, the total survival of medium-sized trees, were very little affected by the hurricane. To some extent, release of small trees might have offset the effect of increased mortality and decreased growth of large trees, but this mechanism appears to have had minor importance relative to the endurance of large subcanopy trees (16 - 40 cm dbh). In our simulations, none of the individual changes in recruitment, growth and mortality brought about by Hurricane Kate was sufficient to result in significant changes in the asymptotic population growth rate.

Slightly increased simulated mortality of trees 16 - 40 cm dbh over the "open" canopy period resulted in a significant decrease in the projected asymptotic population growth, despite increased tree recruitment and growth. This suggests that recurrent disturbance by hurricanes of higher intensity than Kate could compromise the local persistence of *Fagus grandifolia* in these

forests. However, NOAA records (Jarvinen et al. 1984) indicate that while moderately intense storms like Kate are prevalent, high-intensity hurricanes are extremely infrequent in the northern Gulf of Mexico Coastal Plain. Only one high-intensity hurricane (Camille in 1969) has been recorded over more than a century in this whole region, from northern Florida to eastern Texas. In contrast, in the Florida peninsula, where *Fagus grandifolia* is absent, high-intensity hurricanes with maximum sustained windspeeds over 200 km/hour have occurred frequently (Jarvinen et al. 1984).

Neither the recovery nor the complementation hypotheses were supported by our analysis. Estimated asymptotic population growth in the "open" canopy phase was not < 1. A caveat is needed concerning the recovery hypothesis. In our conceptual model, this hypothesis refers to a process that would result from increased population growth under closed-canopy conditions. Although this hypothesis is not supported, some resilience (Pimm 1984) must be involved in the perceived population-size stability in the "open" canopy period because this phase starts with a pulse of increased mortality. If our results are correct, population size of *Fagus grandifolia* is not controlled by recurrent hurricane disturbance (a density-independent factor), either directly, via damage and mortality, or indirectly, via increased competition with light-demanding tree species.

Although the observed patterns conform to the resistance hypothesis, our data leave some room for the release hypotheses. A mechanism involving release was proposed by Foster (1988) as an explanation for the presence of *Fagus grandifolia* and *Tsuga canadensis* in a hurricane disturbed forest in New England. It is possible that our estimate of asymptotic population growth for the

"closed" canopy period might be influenced by long-term effects of previous hurricanes. Because our data excluded all individuals with dbh < 2 cm, our recruits come from seedlings that predate the beginning of the observations. As these recruits could have been exposed to open canopy conditions created by the 1941 hurricane, our 1978-84 data could overestimate the recruitment rate expected over a long period of "closed" canopy. In our simulations, however, λ was robust up to about 3 fold reductions in recruitment rate, and further reductions produced relatively small decreases in λ. This result, along with the known shade-tolerance of *F. grandifolia*, suggest that a declining trend would be unlikely in the "closed" canopy phase. Another problem is that the asymptotic population-size stability for the "open" canopy period could be an artifact of the truncation of our sampling period. By 1992, most of the delayed hurricane mortality had already occurred, but many understory trees were still exhibiting increased growth because the canopy had not yet closed. However, in our simulations the effect of increased growth rate and decreased mortality of small trees was not enough to increase λ significantly, even without hurricane mortality. In addition, our data do not allow us to strictly rule out the possibility that the hurricane prompted a pulse of seedling recruitment, although no field observations suggested this possibility (W.J. Platt personal observation).

Projected stable size-class distributions were monotonic decreasing, resembling the pattern of the observed distributions. However, significant differences occurred between observed and projected frequencies in several size classes, and between the two stable distributions obtained. This suggests that even though hurricanes would not compromise the asymptotic stability of population size, they recurrently modify both the transient and (slightly) the

stable size-class distributions. In both the "closed" and the "open" canopy phases, the population size would remain stable given the respective stable size-class distributions. This, however, does not entail that transient population behavior under alternated "closed" and "open" canopy phases must result in persistence (Caswell and Werner 1978). In our simulations, however, the asymptotic population growth rate was very close to stability for all disturbance regimes. While persistence of the population would not be compromised, its structure would slightly fluctuate over time. In addition, variability in hurricane effects (especially associated with hurricane intensity), and in the environment during both closed and open canopy periods, might affect the demographic rates beyond the variability exposed by our analysis.

Overall sensitivities of population growth to changes in the transition probabilities were lower for *Fagus grandifolia* in both the "closed" (S = 0.57) and the "open" canopy (S = 0.62) phases than for some equilibrium populations of tropical trees. Caswell (1989) calculated S = 1.07 for the population of *Pentaclethra macroloba* studied by Hartshorn (1975), and S = 0.66 - 1.35 for several populations of *Astrocaryum mexicanum* modelled by Piñero et al. (1984), and we obtained S = 1.70 for the model of *Araucaria cunninghami* presented by Enright and Watson (1991). This suggests that perturbations of the life cycle required to move a population away from equilibrium would be greater for *F. grandifolia* in Woodyard Hammock than for those tropical trees.

Changes in recruitment appeared, in our analysis, to have a minor influence on the population growth rate of *Fagus grandifolia*. This result supports the hypothesis of Harcombe et al. (1982) that successful regeneration (in the short term) is not likely to be critical for the local persistence of *F.*

grandifolia. Marks (1975) suggested that *F. grandifolia* is "ill adapted to regenerate in the open". Poulson and Platt (1989, 1995) suggested that, despite the ill-adaptation, this species would persist even under high rates of gap formation, because the light environment in the forest is heterogeneous enough to provide the necessary microsites for regeneration. These authors, and Canham (1988) suggested that population size would fluctuate with changes in the frequency of regeneration. In contrast, our results suggest that, for the fraction of the population ≥ 2 cm dbh, the effects of variation in regeneration are likely to be buffered by more influential vital rates. According to our results the vital rates most critical for the apparent persistence of *F. grandifolia* in Woodyard Hammock were the survivorships of large understory and of small overstory trees. Under the "closed" canopy conditions survival in these size classes would be associated with shade tolerance. Poulson and Platt (1995) pointed out that survival and growth of these understory trees is related to their ability to project nearly horizontal branches towards canopy gaps. High survival of the hurricane might be related to a relatively large trunk diameter for a given height (Peters and Platt 1995), and to high branch elasticity reducing the risk a tree has of being pulled down or broken by falling neighbors (W.J. Platt personal observation).

The critical vital rates for population persistence or growth changed very little as a result of the hurricane. There was, however, a swap between the relative contributions to λ of P, the rate of survival in the same size class and G, the rate of survival and growth to the next class for the 2 - 4 and 4 - 6 cm dbh classes (saplings). In the "closed" canopy scenario, small changes in P for these size classes had a larger effect on λ than the same proportional changes

in G, and the reverse occurred in the open canopy scenario. If there was a trade-off between sapling growth and survivorship, population growth would be maximized with respect to these two vital rates if survivorship was increased during the "closed" canopy phase, even if at the expense of growth, while growth was increased during the "open" canopy phase, even if at the cost of a lower survival.

The same general pattern of life-cycle sensitivity we observed for *Fagus grandifolia* in Woodyard Hammock was found in most matrix-model studies of tree demography. Population growth of forest trees appears to be most sensitive to survival, less sensitive to tree growth, and largely insensitive to fecundity (Harcombe 1987, Enright and Watson 1991, Silvertown 1993). In fact, Gottelli (1991) suggested that this pattern of sensitivity may be characteristic of the wider class of organisms with long life-span, indeterminate growth and reproduction restricted to the larger size classes. This generality suggests that conceptual models of forest dynamics (or other communities dominated by long-lived perennials) should not rely mainly on the regeneration niche concept (Grubb 1977), as survival rather than regeneration appears as critical for the persistence of many tree populations.

A large contribution to population growth of total survival rate in the intermediate size classes (the large pre-reproductives and small reproductives) appears to occur frequently among forest trees and herbs (Hartshorn 1975, Piñero et al. 1984, Burns and Ogden 1975, Caswell 1986, 1989, Enright and Watson 1991, Horvitz and Schemske 1995). This suggests that traits associated with survival of large understory individuals would often be under high selection pressure (Caswell 1989). For the case of *Fagus grandifolia* in the

Coastal Plain, these traits include those resulting in shade tolerance and in tolerance to canopy disruption by moderately intense hurricanes. Survival of these storms by understory individuals would be largely dependent on their ability to withstand the collapse of neighboring canopy trees. This capacity, in combination with shade-tolerance, would also be advantageous in forests exposed to low rates of canopy disturbance by allowing large understory individuals to succeed fallen canopy trees in single tree-fall gaps. Thus, traits conferring *F. grandifolia* its shade-tolerance and its resistance to canopy disruption might have remained linked during confinement of this species to the southern Coastal Plain during Pleistocene glaciations (Delcourt and Delcourt 1987), and its subsequent northward expansion.

General Conclusions

OBSERVED HURRICANE EFFECTS

Along the coastal plain of the northern Gulf of Mexico, stands of the Southern Mixed Hardwood Forest have been affected by a hurricane regime characterized by high storm frequency (4-6 per century) and relatively mild storm intensity (windspeed < 200 km/h). In contrast, natural catastrophes, such as very intense hurricanes or crown fires, appear to be extremely rare in these forests. In Woodyard Hammock, Hurricane Kate damaged extensively the canopy increasing the light levels in the understory. As a result of this disturbance, the dynamics of the forest changed markedly. In the seven years that preceded Hurricane Kate, recruitment of trees into the understory was scarce and restricted to a few species, and rates of growth and survival were low for understory trees and high for overstory trees. In the seven years that followed Hurricane Kate, recruitment of trees into the understory increased, largely as a result of release of advance recruits present under preexisting, localized canopy gaps. In addition, growth and survival of understory trees increased, while growth and survival of overstory trees decreased. These changes represented a shift in the proportion of captured resources from the overstory to the understory strata. However, as well as in the understory, most trees in the overstory survived. The demographic significance of release of understory individuals and survival of adult or pre-adult trees appeared to differ among species.

The dominant hardwood species in Woodyard Hammock, *Magnolia grandiflora*, *Fagus grandifolia*, *Liquidambar styraciflua*, *Nyssa sylvatica*, and *Ilex*

opaca, appeared to depend mainly on survival of adult or pre-adult trees for persistence in the forest. *Magnolia grandiflora*, as well as *Nyssa sylvatica*, had little recruitment into the understory both before and after the hurricane, and no increase of growth or survival of understory individuals after the disturbance. Survival of overstory individuals of these species was high, and accounted for their permanence as community dominants. After Hurricane Kate, *Fagus grandifolia* had increased growth and survival of saplings and increased growth of understory trees. However, our detailed demographic analysis of this population showed that the most critical vital rate for its persistence was the survival of large understory and small overstory trees, a vital rate which was essentially not affected by the disturbance. Demographic patterns of *Ilex opaca* were similar to those of *F. grandifolia*, suggesting that survival of adults or pre-adults would also be critical for this species. *Liquidambar styraciflua* had substantially increased recruitment, growth, and survival of understory trees, and also high survival of overstory trees. This species has clonal habit and performance of its understory ramets is known to depend to some extent on root reserves. These characteristics suggest that, although release of understory individuals may contribute, persistence of *L. styraciflua* in Woodyard Hammock would critically depend on survival.

Three dominant species, the understory *Ostrya virginiana* and *Carpinus caroliniana*, and the overstory *Pinus glabra*, appeared to depend on periodic release of understory individuals by large-scale canopy disruptions. These three species accounted for most of the increase of recruitment occurred in Woodyard Hammock after Hurricane Kate. For *Ostrya virginiana* and *Carpinus caroliniana*, recurrent release would be critical for long-term persistence as

adult individuals of these species are likely to be outgrown by longer-lived trees of overstory species. Mortality of adult *Pinus glabra* was high before the hurricane and the surviving trees were largely decimated by the disturbance. This pattern essentially resulted in the replacement of one cohort of *P. glabra* by another, and persistence in the forest appeared to depend critically on the rapid growth of the released understory individuals.

In Woodyard Hammock, the changes in tree recruitment and survival that followed Hurricane Kate resulted in rapid changes of relative species densities in the understory. However, these changes occurred essentially without invasion or extinction of tree species at the stand level. This stability of tree species composition suggested that, in Southern Mixed Hardwood Forests, hurricanes would not release any resources that alien species could exploit, and that competitive exclusion would occur rarely, if ever, in the intervals between hurricanes. However, the existence of alternative life-history strategies to cope with hurricane disturbance suggests that recurrent hurricanes are involved in the coexistence of multiple tree species in these forests.

HURRICANES AND TREE-SPECIES COEXISTENCE

Continued coexistence of multiple species in a community could be explained in terms of the conditions for persistence of the individual species. Although population persistence would depend upon completion of the whole life cycle (at least at some relevant spatiotemporal scale), those vital rates making the largest contribution to the asymptotic population growth are potentially the ones most restrictive for population persistence (Caswell 1978, 1989, de Kroon et al. 1986). Therefore, a necessary condition for continued species coexistence is that the most critical vital rates in each population are

not compromised by the environment or by interactions with companion species. Based on our results from Woodyard Hammock, we hypothesize that regeneration or performance at early stages of the life cycle would be typically most limiting for short-lived, light-demanding tree species, while survival of adults or pre-adults would be typically most limiting for long-lived, shade-tolerants.

The Southern Mixed Hardwood Forest in Woodyard Hammock was composed of a somewhat stable matrix dominated by overstory hardwoods, dotted with more dynamic patches dominated by *Pinus glabra* or understory species such as *Ostrya virginiana* and *Carpinus caroliniana* (Peters and Platt 1996). Coexistence of these two structural elements appeared to result from the characteristics of the hurricane regime. Species dominant in the dynamic patches appeared to depend for persistence on frequent release of understory individuals by frequent hurricane disturbance. Prevalence of advance regeneration among these species suggests that hurricanes are frequent enough so that local extinction of adults is unlikely. In contrast, the dominant overstory hardwoods appeared to depend critically on tree survival for persistence in the forest. Modelling results for *Fagus grandifolia* suggested that this critical survival has not been compromised in Woodyard Hammock because the hurricanes that have affected this forest were not intense enough. The resulting pattern is somehow akin to the intermediate disturbance hypothesis (Connell 1978, Huston 1979); increased hurricane intensities could override the resistance of dominant overstory hardwoods compromising their persistence, while decreased hurricane frequency could compromise the persistence of *P. glabra* and the understory species as a result of lower frequency of release.

AN EVOLUTIONARY HYPOTHESIS ON THE EFFECT OF FREQUENT DISTURBANCE

The expected importance of release in forests frequently disturbed by wind is likely to depend on the proportion of the canopy that is disrupted, which in turn is influenced by the characteristic disturbance intensity and by the resistance of the canopy trees. We hypothesize that the higher the characteristic disturbance intensity the more likely it becomes that life-history strategies dependent on release of young trees would prevail over those dependent on survival of older trees (Figure C.1). At an evolutionary time scale, frequent hurricane disturbance would select for traits that result in rapid gap capture (Denslow 1980, 1984). However, chronic hurricane disturbance is also

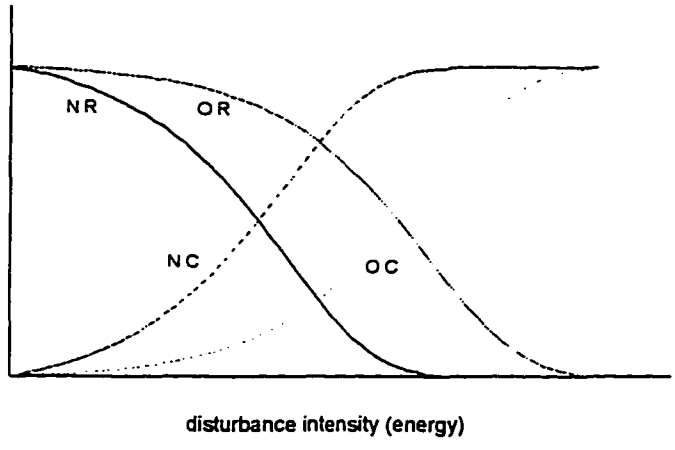

FIGURE C.1. Hypothetical association between characteristic disturbance intensity and expected relative importance of life-history strategies based on resistance and on release after a short and a long history of exposure to a regime of frequent disturbances. Disturbance intensity is measured by the amount of energy spent to destroy biomass, and the relative importance of each strategy by the proportion of the total biomass it accounts for in the community. In the labels of the hypothetical curves N stands for short and O for long history of frequent disturbance, and R stands for resistance and C for release.

likely to select for resistance traits that result in reduced damage and increased survival of large trees. If such resistance adaptations appear, they are likely to prevail over the adaptations for rapid gap capture. Therefore, we hypothesize that, given a characteristic disturbance intensity, the longer the forest has been exposed to the disturbance regime the more likely it becomes that life-history strategies dependent on resistance would increase in relative importance (Figure C.1). As the evolution of resistance is likely to be more constrained at higher disturbance intensities, increases in expected importance of resistant life-history strategies with the evolutionary history would be smaller at high disturbance intensity. Under this hypothesis, replacement of short-lived, fast-growing trees, dependent on frequent release, by long-lived, slow-growing trees dependent on survival, is predicted to occur at the evolutionary time scale.

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Appendix: Letter of permission

United States Department of Agriculture
Forest Service
Southern Research Station
200 Weaver Boulevard
P.O. Box 2680
Asheville, NC 28802

Date: October 25, 1996

Mr. William Bennett Batista
Louisiana State University and
Agricultural and Mechanical College
Department of Biology
502 Life Sciences Building
Baton Rouge, Louisiana 70803-1703

Dear Mr. Batista:

This letter is to inform you that permission has been granted to reprint the article "Old-growth Condition in the Southern Mixed Hardwood Forest Type" by W.B. Batista and W.J. Platt. If you have any questions, please contact me.

Sincerely,

Carol Ferguson
Communications Group Leader

Vita

William Bennett Batista was born in Chattanooga, Tennessee, on July 6, 1955, to a couple of Argentine students. Moved at early age to Argentina, he grew up in Buenos Aires where he obtained a degree in agriculture in 1979. In the early 1980's he lived in the Chaco region of northeastern Argentina working as a trainee for the Instituto Nacional de Tecnología Agropecuaria. He met his wife, María Zorzón, in Reconquista, in 1983. In 1984 he moved back to Buenos Aires to work in a research program on the ecology of Pampean grasslands under the guidance of Rolando J.C. León at the Universidad de Buenos Aires. Upon creation of the graduate school of agriculture in this university, he enrolled and completed his Magister Scientiae degree in 1991. He has published six scientific papers and has taught undergraduate and graduate courses of ecology and vegetation science at the University of Buenos Aires, and graduate courses in statistics at the Instituto Nacional de Tecnología Agropecuaria and the Universidad de Balcarce, Argentina. In 1992, he arrived in Baton Rouge to work on his doctoral program under the direction of William J. Platt at Louisiana State University. The doctor of philosophy degree will be conferred in December, 1996.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: William Bennett Batista

Major Field: Botany

Title of Dissertation: Role of Hurricane Disturbance in the Dynamics of the Southern Mixed Hardwood Forest: A Case Study in Northern Florida

Approved:

William J Platt
Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

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Date of Examination:

September 11, 1996